FIELD AND LABORATORY STUDIES OF THE BEHAVIOUR OF THE SWIMMING CRAB *LIOCARCINUS DEPURATOR* (LINNAEUS)

by

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A thesis submitted for the degree of

DOCTOR OF PHILOSOPHY

at the

UNIVERSITY OF GLASGOW

DEPARTMENT OF ZOOLOGY

1985

CONTENTS

List of Tables

List of Figures

List of Figures

List of Figures

List of Plates

ACKNOWLEDGEMENTS

I wish to thank my supervisor, Dr Felicity Huntingford for her helpful advice and discussion throughout this project; and particularly for guidance regarding the organisation and presentation of this thesis.

Dr I.G. Logan gave up many hours of his time to help with computational aspects of this work and for this I am extremely grateful. Dr F. Critchley advised and gave computational help with the frame by frame analysis and Sheila Robertson typed the manuscript quickly and accurately.

Iain Logan, Michael Burton, Ian Knight and Brian Mullins gave up their spare time to assist with the diving work, often under the most arduous conditions. Fieldwork would not have been possible without this assistance.

My parents have encouraged and supported me throughout my research and have my deepest gratitude.

This work was financed by a research grant from the Department of Education for Northern Ireland.

SUMMARY

Field observations were made at Loch Sween in an attempt to describe the behaviour and ecology of L. depurator. Abundance varied over time with peak abundance occurring during periods of warm water. Peak densities of 1 crab/7m^2 were observed but average density was much lower at 1 crab/25m^2. Some evidence was obtained for migration from the study site similar to that reported for other species. Tagging studies revealed no long term site attachment. Populations were found to be sex biased in favour of male crabs during summer months and individuals were most commonly observed within 1m of the nearest conspecific. Ovigerous crabs were observed in two distinct phases between April and September and recruitment of juvenile crabs occured in early spring. Observations on food and feeding behaviour showed L. depurator to be a predator of sessile or slow moving benthic macroinvertebrates. The main types of escape response were observed and discussed. The incidence of physical damage and naturally occurring aggression in the field were low.

Investigation into the locomotor activity of individual swimming crabs in the laboratory showed that shallow water (<9m) crabs displayed significant cyclic locomotor activity while deep water (>30m) crabs displayed arhythmic activity.

CHAPTER 2

1. Regular field observations using SCUBA techniques were made at two sites in Loch Sween (Argyllshire) in an attempt to describe the behaviour and ecology of L. depurator as a background for subsequent laboratory studies.

2. Abundance of animals varied over time with peak abundance occurring during the months of September-November corresponding to periods of warm water. Local variations in visibility did not seem to affect local abundance.

3. During periods of peak abundance, densities of 1 crab/7m^2 were observed but average density was much lower at 1 crab/25m^2.

4. There was some evidence for migration from the study site, similar to that reported for other species. Transect studies failed to yield any information on these movements and it is postulated that further studies using ultrasonic tagging and tracking techniques may elucidate the movement patterns of individuals.

5. Claw tagging of individuals with Floy Co. Spaghetti Cinch-Up tags revealed that there is very little long term site attachment by L. depurator at Loch Sween. Individuals within the study area were continually changing even though in the short term, local

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5. Claw tagging of individuals with Floy Co. Spaghetti Cinch-Up tags revealed that there is very little long term site attachment by L. depurator at Loch Sween. Individuals within the study area were continually changing even though in the short term, local

abundance remained relatively constant. A very low level of continuity was maintained within the study area by tagged individuals returning periodically. It is postulated that this is of little significance due to the low level of continuity.

6. During summer months local populations were found to be biased in favour of male crabs. Transect studies failed to identify differential female/male migration and again it is suggested that further tracking studies using ultrasonic tags may be needed to elucidate these movements of individuals.

7. Individuals were most commonly observed within 1 metre of the nearest conspecific and localised densities of up to 3.3 crabs/m^2 were reported. These local aggregations did not appear to be formed by single sex groups.

8. Ovigerous crabs were observed in two distinct phases between April and September. This observed brooding period is substantially different from that reported in some studies and similar to others. It is suggested that this may reflect inadequate sampling of certain areas and the brooding period of L. depurator may be longer than previously stated.

9. Recruitment of juvenile crabs occurs in early spring but the subsequent increase in adult crabs is caused by movement of large crabs into the study area, not by growth and maturation of the early spring immigrants.

10. Habitat utilisation by L. depurator appears to be non-random at Loch Sween. Crabs were most commonly found totally covered or alert and standing in exposed areas. It is suggested that this habitat utilisation is associated with feeding and anti-predator behaviour.

11. Observations on food and feeding behaviour showed L. depurator to be essentially a predator of sessile or slow moving benthic macroinvertebrates, a diet similar to that of many larger crustaceans. However, L. depurator also has the ability to capture larger active prey through its ability to swim at great speed.

12. L. depurator showed three main types of escape response to approaching divers and these were taken as normal anti-predator responses. The adaptive significance of each of the responses is discussed.

13. The incidence and possible causes of physical damage shown by crabs in the field is discussed. Levels of physical damage in the field are lower than those observed in laboratory populations, probably due to lower density of crabs in the field.

14. A number of naturally occurring social aggressive interactions were observed in the field. These interactions were described and the results provide a basis for the study of similar aggressive interactions in the laboratory. The observed incidence of such aggression in the field was very low.

CHAPTER 3

1. Locomotor activity of 34 individual swimming crabs (L. depurator) was studied in the laboratory using light beams and photoelectric cells to detect activity.

2. Acclimatisation to the experimental apparatus was investigated. A 24 hour acclimatisation period was employed during this study and was chosen in light of the available literature and personal communication (Morris, Taylor). The results of the present study indicate that for L. depurator, a 24 hour acclimatisation period is more than adequate.

3. 3-dimensional plots of activity, time and position in tank were produced as a visual guide to activity patterns produced by individual crabs and as a check on preferential attraction towards areas of the tank. No such preferential attraction which may have affected subsequent analysis was observed.

4. Spectral analysis using autocorrelation and Fourier transformation was employed in order to detect any rhythmicity present in the time-series data.

5. Crabs from two different types of site were studied; a shallow water site (3-9 metres) affected by tidal considerations and with plentiful cover available in terms of rocks and areas of thick kelp; a deep water site (30 metres) not affected by tidal

considerations, with an undulating muddy substrate and much less available cover than the shallow water sites.

6. Three different lighting regimes were employed.
   a) Normal laboratory lighting (LD 12:12), 12 hours of light followed by 12 hours of darkness.
   b) Constant darkness (LD 00:24)
   c) Constant illumination (LD 24:00).

7. Significant rhythmicity was displayed under all three lighting regimes, indicating that the activity displayed under LD 12:12 was not induced by the cyclic laboratory environment.

8. Shallow water crabs (83%) displayed significant cyclic locomotor activity while deep water crabs (86%) displayed arhythmic activity.

9. A predominant 25 hour cycle was displayed by shallow water crabs in which peak activity corresponded with 'expected' night time flood/high tide.

10. These results were discussed in relation to the nature of the environment of each of the two types of collection site. It is postulated that the patterns of activity shown by shallow water crabs may be an adaptation to life in a cyclic environment, allowing efficient foraging without a greatly increased risk of predation.

11. The relevance of these findings to the design of subsequent experiments is discussed and it is suggested that arhythmic (deep water) crabs should be used in subsequent laboratory experiments in an attempt to reduce the number of possible variables.

CHAPTER 4

1. 107 paired inter-male interactions, carried out in a round-robin series between 47 individual crabs were recorded on videotape from which a qualitative description of the agonistic behaviour of L. depurator was obtained.

2. Flow diagrams of the main sequence of events were prepared for initiators, responders, eventual winners and eventual losers. Few differences were observed in the overall pattern of these flow diagrams.

3. Four main categories of interaction were observed and the incidence of each discussed. The four categories were, fights settled by stationary display; fights settled by a single approach/retreat; fights involving multiple bouts of approach/ retreat; fights involving physical contact between contestants.

4. Behaviour patterns were described for a number of isolated individuals and compared with the behaviour shown by interacting pairs of crabs. The behaviour shown by single crabs was markedly different from that of paired interactants.

5. Determinants of the initiation and outcome of interactions were discussed. Small crabs were just as likely to initiate an interaction as large crabs and there was no significant difference between initiators and responders in terms of winning or losing an interaction.

6. Smaller crabs were capable of winning interactions but only when size difference between individuals was small.

7. Interactions ranged from eight frames up to 266 frames in length with fights between large size class crabs lasting longer than fights of any other category. The size of the smaller crab was shown to be the most important factor affecting fight length.

8. Comparison of behaviour shown by individual crabs from interaction to interaction showed that the majority of fights followed a set pattern and that within any given interaction, both crabs showed very similar behaviour patterns irrespective of the SDI* or the final outcome of the interaction. The implications of this matching behaviour were discussed.

9. Comparisons made between fights of different lengths and also with the different length fights split into winning, losing, initiating and responding categories showed that very few differences existed in the proportion of behaviour patterns shown in any of the categories examined. The differences which did exist were minor and did not reflect major differences in organisation between the different categories.

10. When fights were divided into segments there was no evidence to suggest that progressive escalation in intensity occurred in any of the categories studied. The behaviour patterns occurred evenly over all segments of a fight and those trends which did exist tended to reflect arbitrary distinctions concerning the beginning and the end of an interaction.

CHAPTER 1

GENERAL INTRODUCTION

In the class Crustacea there are eight sub-classes and thirty recent orders. The class contains about 26,000 species, but the only sub-classes with more than 10% of this total are the Copepoda (4,500 species) and the Malacostraca (18,000 species). Thus the Malacostraca contains some 70% of all crustacean species. Similarly, within the Malacostraca, most of the species are contained within three orders, the Amphipoda (3,600 species), the Isopoda (4,000 species) and the Decapoda (8,500 species). The crabs, shrimps and lobsters are contained within the Decapoda, but with a total of about 4,500 species, the majority of decapod species are crabs. Thus in terms of numbers of species, the crabs are one of the largest groups of the crustacea. Due to their abundance, ease of collection and convenient size, more is known about crabs than about any other single group of crustaceans. In addition, the true crabs or brachyurans also show the most advanced traits of all crustaceans in both morphological and social behaviour (Warner, 1977).

Essentially, the brachyurans are members of a warm water fauna, as it is in tropical regions that crabs reach their greatest diversity in numbers of species and sub-species. Nevertheless, a significant number of crab species inhabit temperate waters. Sixty seven species, for example, have been recorded from the waters surrounding the British Isles where they occur in a wide range of habitats and depths, from the intertidal region to the deep waters beyond the continental shelf (Ingle, 1980). However, despite the considerable attention the crustacea have received, our present knowledge of the N.E. Atlantic crab fauna is incomplete (Ingle, 1980). Precise information on the geographical distribution of the majority

of species that occur in British waters is not yet available, the bathymetric range of many species is still poorly documented and the ecology of only a few is known in detail.

Of the 59 endemic species of true crab found in British waters (Ingle, 1980) almost one quarter (15 species) are contained within the family Portunidae. Fifteen is a manageable number for a cross species comparison, but of these species, only Carcinus maenas, the common shore crab, has received more than a passing interest. Of the other members of the family, Liocarcinus depurator, the common swimming crab is perhaps the most common species being abundant in many areas and reported from all Marine Census Areas around the British Isles (Ingle, 1980). Its wide distribution and abundance therefore make L. depurator suitable as a reference point for any cross species comparison within the Portunidae as well as studies concerning interspecific competition. The literature on L. depurator however, is sparse. Only three reports deal with the distribution of the crab (Allen, 1967; Boidot, 1971; Ingle, 1980) while the other studies report on its predators (Johnstone, 1907) water permeability (Rudy, 1967) respiration (Uglow, 1973) and temperature effects on developing eggs (Wear, 1974). That L. depurator is an important member of many sub-littoral communities (Dipper and Mitchell, 1979) has been accepted for some time. It is therefore surprising that so little attention has been paid to the general biology and ecology of the crab.

Initial, casual observations in the laboratory have shown L. depurator to be a highly aggressive animal. This aggression takes the form of a number of recognisable postures including displays in which the vivid

blue markings on the dactylus of the fifth pereiopods are prominent. Other, less common tactics are observed during fights which escalate to a physical level but in all cases bouts of aggression have a well defined beginning and end, in that the initiators of aggression can be clearly identified, as can the winners and losers of each bout.

A detailed study of the exchange of signals during a fight may provide valuable information allowing current ideas on the adaptive significance of details of animal fights (Maynard-Smith, 1982) to be tested. Such functional questions require that the behavioural characteristics shown in the laboratory are not artefacts. Therefore, in addition to the laboratory observations, field studies are essential in order to allow assessment of the relevance of laboratory results to the behaviour of animals under natural conditions. Similarly, valid extrapolation from laboratory to field observations require knowledge of daily rhythms of activity, as this will dictate many aspects of social systems shown by the animals (Hazlett, 1975). This investigation, therefore, takes the form of a series of closely related laboratory and field studies, whose aim is to fill in some of the gaps in our knowledge of the biology of L. depurator. The work is presented in three sections.

1. Field studies on the behaviour and ecology of L. depurator.
2. Locomotor activity patterns shown in the laboratory.
3. A study of intraspecific aggression shown in the laboratory.

CHAPTER 2

FIELD STUDIES ON THE ECOLOGY AND BEHAVIOUR

OF THE SWIMMING CRAB

LIOCARCINUS DEPURATOR

2-1 INTRODUCTION

2-1.1 METHODS OF COLLECTING FIELD DATA

Although crustacean biology in all its aspects has been intensively studied in the laboratory, there are few cases in which the laboratory findings have been supplemented by, and compared to field data. This raises the possibility that laboratory studies are of artefacts or that certain findings may depend on the abnormality of the laboratory situation. There is therefore no reason to assume that these results have much relevance to how animals behave or react in the wild. Given the implications of this assumption, there is a need to study how animals behave in the field and it is not surprising that the exceptions to the above generalisation include the commercially important species such as Cancer pagurus, the edible crab, Homarus gammarus, the lobster, Nephrops norvegicus, the Norway lobster, or species which are readily observable in the field such as Carcinus maenas, the shore crab. Such field studies as have been carried out fall into two categories; studies involving remote sampling techniques and those in which direct observations have been made.

2-1.2 REMOTE SAMPLING

Most of the research into the ecology of the commercially important species has been carried out by remote sampling and was designed to provide information concerning population size and local density,

growth patterns, sex ratio and distribution of individuals with respect to topography. This kind of information is necessary for any effective fishery policy. A number of remote sampling techniques exist and include trawling, creel-fishing, telemetry and mark-recapture techniques.

During the period 1960-1962, crab tagging experiments were carried out for the crab Cancer in the Eyemouth Fishery District (Mason, 1965). These experiments were designed to study the growth and movements of crabs and to study the fishing mortality. Early experiments involved the attachment of a metal tag to a claw by copper wire, a time consuming and difficult procedure. The major drawback of these claw tags however, was that no information on growth could be obtained as the external tag was cast off during a moult, along with the old exoskeleton. This also imposed a limitation on the duration of observations. The problems were overcome by the suture tag method developed by Van Engle and described by Butler (1957) and Mistakadis (1957), which allowed a numbered tag to be attached to a crab and retained through each moult. This was achieved by passing the tag through the cuticle of the crab, along the moult line. During the moult the exoskeleton splits along this line leaving the tag in place in the newly formed exoskeleton underneath. In his comprehensive study, Mason (1965) released 1531 tagged Cancer on the crab fishing grounds over a period of one year. Tag returns were mainly from commercial fisherman with over 390 tags being returned within 20 months of the first batch of releases. The results of this study supported the widely held view that larger crabs move offshore in autumn and inshore in spring. There was also some suggestion that males moved only at random while females undertook

longer movements connected in some way with the breeding ecdysis cycle. One female was recaptured 126 miles from the point of release. These results agreed with those obtained by Meek (1913), and Mistakadis (1960). Edwards (1964, 1965, 1972) provided similar information on movements of Cancer on the south coast of Ireland. Many more tagging studies have been undertaken since these early experiments, with the emphasis on migration patterns of lobsters (Cooper and Uzmann, 1971; Dow, 1974; Watson, 1974) and Nephrops (Chapman and Rice, 1971).

In a more recent study, movement and dispersion patterns of the commercially important giant freshwater prawn Mac robrachium rosenbergii were investigated (Peebles, 1979). This study attempted to identify important social mechanisms influencing access to resources and therefore survival and growth, the underlying social structure being deduced from movement and dispersal patterns. The remote sampling techniques used were necessary in this case as the prawn is normally nocturnally active and inhabits streams and ponds where water turbidity prevents direct observation.

Prawns in commercial tanks were tagged with small acoustic transmitters and tracked using underwater receivers. Information on day to day movement in these large tanks (36 x 99 metres) was obtained by monitoring the position of individuals every 24 hours. A quadrat sampling method was used to gather data on water depth, mud depth, and number of animals. This study revealed that females moved greater distances at night than males, and females exhibited a weaker tendency than males to return to a home site. Reproductive condition and proximity to ecdysis were related to the distance

females moved at night. Females with eggs moved greater distances than other females and the closer an animal was to ecdysis, the greater its movement. Peebles (1979) concluded that these females may have been seeking a suitable mate to protect them during the vulnerable period just before and after moulting.

Environmental heterogeneity, productivity and habitat utilisation differed between different ponds. In ponds with a more heterogeneous environment, late premoult and early postmoult prawns apparently avoided hard intermoult and early premoult prawns by occupying a less preferred habitat of deep, soft mud. This movement of animals near ecdysis, into an area not preferred by intermoult animals could reduce the hazards of an encounter with intermoult animals. If animals near ecdysis cannot avoid prolonged encounters with intermoults, they usually suffer extensive body damage often resulting in death (Peebles, 1980). Therefore, ecological conditions play an important role in determining the probability of an animal surviving a moult and hence growth. This was emphasised by significantly increased productivity in the pond with a more heterogenous habitat in terms of mud depth (Peebles, 1979).

The sonic tags (telemetry) used in this study proved to be an improvement over conventional tags, enabling the position of an experimental animal to be precisely determined at any time. The benefits of this approach include the ability to track an animal continuously, thereby providing information on speed and direction of movement, parameters not instantly or readily available using conventional tagging procedures. Limitations of this approach include the high cost of transmitters and receiving apparatus but

despite this, a number of studies of crustacean movement patterns have been undertaken using these techniques and are becoming increasingly important. These studies include Chapman et al, (1975) on Nephrops and recent similar studies on Hom-arus at Aberdeen Marine Laboratory (Chapman, Pers. Comm.).

Not all of the studies of the distribution and ecology of the crustacea have used tagging procedures. Wolff and Sandee (1971) looked at the distribution and ecology of the decapoda reptantia of the esturine area of the rivers Rhine, Meuse and Scheldt. Their survey included data from a number of sources including grab samples, hauls with a small shrimp trawl, observations from commercial fishing vessels and data derived from the collections of various museums. The data they collected allowed the distribution of 24 species to be identified.

Similarly, Norse and Estevez (1977) looked at population structure and species composition of portunids along salinity gradients in estuarine systems on the coast of Columbia. They sampled using standard shrimp trawls and species composition for benthic and demersal crabs were calculated for each trawl based on abundance and biomass. Differences in landward distribution and abundance were accounted for by differential tolerance to salinity, but competition, predation by fishes, and decreased food availability limited the seaward distributions. Haefner (1978) looked at seasonal abundance of the deep sea red crab in the North-west Atlantic by taking demersal trawl surveys over a period of three years, while Paul (1982a, 1982b) carried out a similar study for swimming crabs of the genus Callinectes on the Mexican Pacific coast.

This is not a complete review of the literature concerning remote sampling techniques. However, it illustrates the different techniques which may be used to study the biology and ecology of crustacea in their natural habitats, the kind of information they provide, and also the range of species and problems to which the have been applied.

2-1.3 DIRECT OBSERVATION

The methods discussed above allow reasonable estimates of relative density and provide a crude indication of gross movements, but with the exception of sonic tagging experiments, provide little or no information concerning distribution and spacing of individuals within the area fished. For this reason, a number of recent studies have employed direct observation in order to obtain more information on spacing patterns, and a greater understanding of behaviour under natural conditions.

Chapman and Rice (1971) carried out a detailed investigation of a small area of seabed occupied by Nephrops in Loch Torridon, Scotland using diving and underwater television. This survey, in addition to information on size and sex composition of the population also allowed the nature, arrangement and density of the burrows to be studied, information which would have been impossible to obtain by remote sampling. Further field studies by Chapman et al (1975, 1979a, 1979b), using television and time lapse photography, have allowed the burrowing behaviour of Nephrops to be described and also allowed the identification of complex emergence rhythms in these animals.

Early work by Broekhuysen (1936), Edwards (1958) and Naylor (1962) suggested that Carcinus may undergo migrations up and down the shore, Dare and Edwards (1981) used closed circuit television (CCTV) underwater to observe the pattern of these intertidal movements of Carcinus across a particular section of mudflat, and to estimate the numbers of crabs participating in such movements. Large numbers of crabs performed daytime tidal migrations up and down the mudflat. Most crabs undergoing these movements were larger than 20 mm carapace width and peak movement of individuals occurred in at least 0.5 m of water thereby possibly helping the crabs avoid predation by gulls or large wading birds. Over the high tide period, most crabs were dispersed over the upper half of the mudflat where crab population densities of 1.8-2.5/m^2 were observed. This study showed that there is considerable scope for investigations of behaviour in the field using CCTV but also identified portability of equipment and variable underwater visibility as disadvantages of the approach.

As an alternative to CCTV and photographic observations, diving techniques may be used, although these also have inherent disadvantages. As with CCTV, poor underwater visibility may present a problem but divers are generally more flexible and as a rule have better visual acuity than any CCTV system. Other problems include an inability to work at depth for long periods of time, difficulties associated with the recording of information gained while underwater, and possible disturbance to the animals being observed. These problems can be overcome under certain circumstances and the information obtained by diver observation in many cases may be extremely valuable.

Snorkel divers were used to study home range, size, extent of daily movement, and extent of day-night movement for marked individual spider crabs (Mithrax spinosissimus, Hazlett and Rittschof, 1975) as a prelude to the study of social systems in the animals. Schriever (1978) looked at the behaviour and biology of the tropical spider crab Stenorhyncus seticornis in the coral reefs of Freeport, Grand Bahama, by saturation diving from the American Underwater Laboratory, Hydrolab. This removed the immediate problems of decompression and allowed observations on the crabs for up to five hours per day. Such saturation diving, as yet rare in the scientific field allowed a very complete study of the biology of this spider crab to be made, and illustrates how important studies by divers may be.

From the information above, it is clear that knowledge about the ecology and behaviour of certain crustacean species is extensive. However, it is equally clear that the species of crabs and lobsters which support a valuable fishery, have recieved most attention at the expense of those species which have little or no commercial significance. This concentration on the commercially important species has a number of important consequences.

1. Data on non-commercial species, which may be of intrinsic theoretical interest may not become available.
2. Information on species which may yet become important economically is not available.
3. Information on species which may interact and compete with commercially important species may be neglected.
4. A valuable comparative dimension to data on important species is not available.

In addition, the nature of the data collected on important fisheries species is problematic in that the data is obtained mainly by sampling from the fishery itself. This usually provides information which has a direct bearing on fishery problems only. Such information may well be important but may not provide a complete or even adequate description of the ecological or behavioural characteristics of the species. As discussed above, direct observation of the animals in their habitat may overcome some of these problems.

2-1.4 OUTLINE OF RESEARCH PROGRAM

The present study is an attempt, not only to fill part of the gap left by the fisheries orientated approach, but also to provide background information for subsequent laboratory studies. It concerns the swimming crab L. depurator, a species which is of some theoretical interest (see Chapter 1) and which is important for a number of reasons.

1. L. depurator is closely related to L. puber, a species of commercial importance.
2. L. depurator is sympatric with and possibly in limited competition with other commercially important species such as Nephrops.
3. L. depurator is a possible candidate for limited fishery exploitation in the future.

This section was designed to provide information on the ecology and habitat utilisation of L. depurator and to describe the behaviour of this species under natural conditions for comparison with results obtained from laboratory experiments. In the time available it was not feasible to carry out a complete quantitative study; consequently many of the results are of necessity presented in a semi-quantitative manner. The specific questions under consideration were as follows.

1. What is the pattern of habitat use by L. depurator?
2. What are local population densities?
3. Are local populations stable or do populations and individuals constantly change?
4. Is there any evidence of long term site attachment and if not, what form do the movements of individuals take?
5. Are local populations uniform in composition or is there evidence of size or sex class aggregation?
6. How do individuals forage and what food items are taken?
7. Are there any breeding and population cycles?
8. What form do social interactions take?

2-2 METHODOLOGY

2-2.1 DESCRIPTION OF STUDY SITES

Field studies were made at two sites of different nature in Loch Sween on the west coast of Scotland (Figure 2.1). The position of the two sites, Eilean Mhartan and Port Lunna are shown in Figure 2.2. Loch Sween was chosen because of its convenience to Glasgow and because the following logistic preconditions were met.

1. Dive site must be readily accessible from the road.
2. Must be accessible at all times of the year.
3. Site must be diveable under all conditions, i.e., site must be sheltered.
4. Water must be relatively shallow to allow considerable time to be spent underwater.
5. L. depurator must occur commonly at the site.

A number of sites other than Loch Sween were investigated, but discarded due to one or more the above conditions not being met.

EILEAN MHARTAN

Eilean Mhartan is situated at the head of Loch Sween and is well sheltered from all directions. The study area was marked at its northerly end by three buoys which had previously indicated the limits of an oyster farm. The area within these buoys is littered with the remains of oyster cultivation trays and this provides a very varied habitat for a rich flora and fauna. The shoreline to the south of

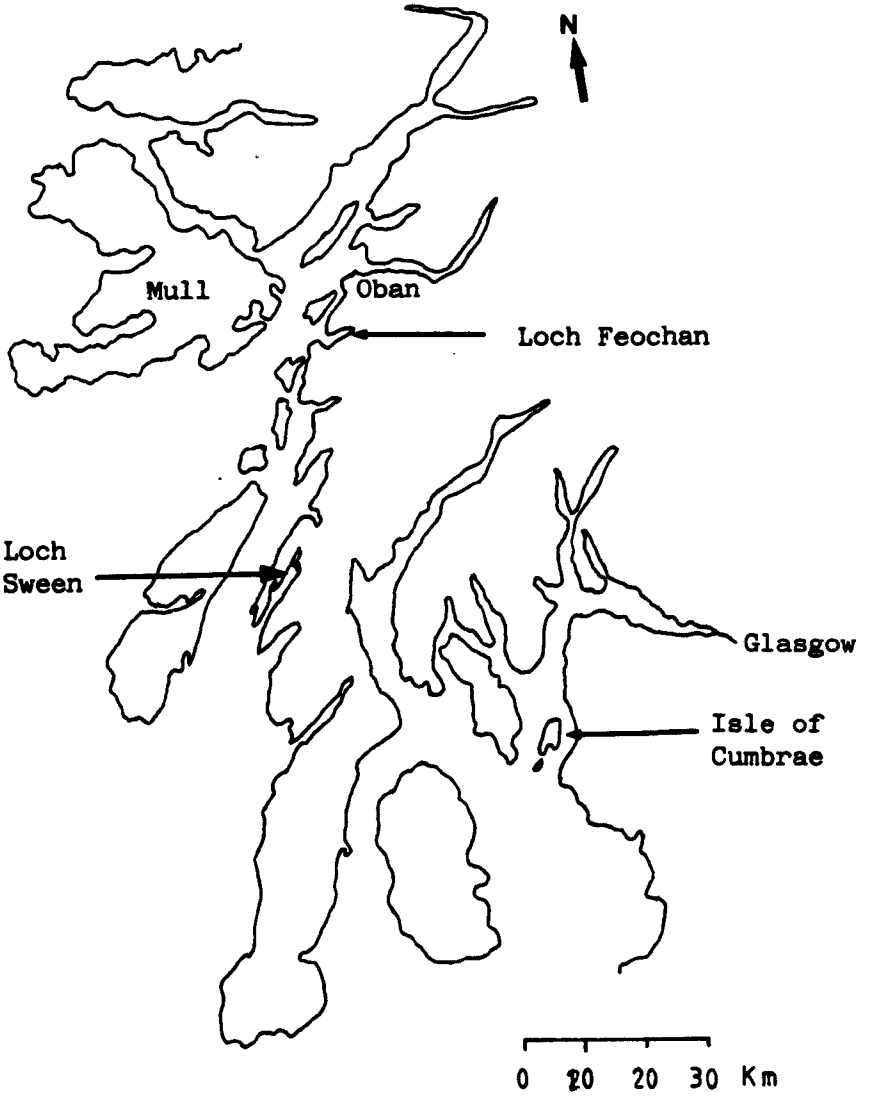


Figure 2.1

Map showing position of collection and study sites in relation to Glasgow.

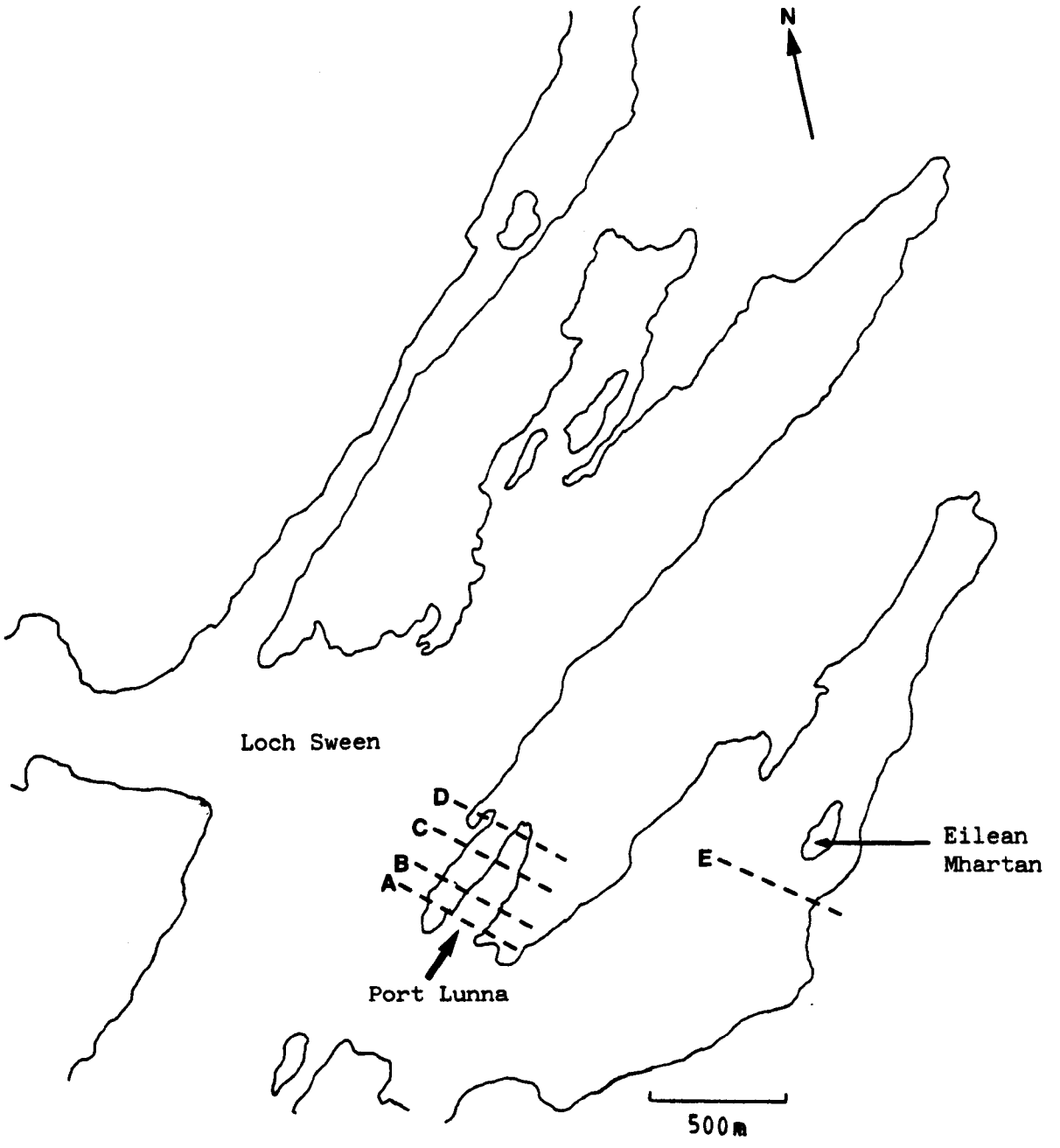


Figure 2.2 Showing position of Eilean Mhartan and Port Lunna in Loch Sween.

Eilean Mhartan is easily accessible from the road by a short walk across a muddy foreshore. A profile of the site along transect line E (Figure 2.2) is shown in Figure 2.3.

Moving directly offshore (Northwest), the shore shelves slowly for 25 metres over a sandy substrate with isolated clumps of Mytelis edulis, the common mussel, and Modiolus modiolus, the horse mussel. This region is also characterised by patches of seaweed, notably Fucus vesiculosus, the bladder wrack and Fucus serratus, the tooth wrack. From a depth of about 2 metres, the shore shelves steeply at an angle of 45° to a depth of 6 metres. (All depths are reduced to Chart Datum.) This slope is comprised of small pebbles and stones with occasional clumps of seaweed and sea-squirts (Plate 2.1). At a depth of 6 metres this slope gives way to a fine silt and mud substrate. Close inshore, clumps of weed and debris scattered over the substrate provide cover for L. depurator and other organisms (Plate 2.2). Moving offshore from the pebble slope, the bottom shelves very slowly to a maximum depth of 11 metres in the middle of the loch. With increasing depth, the clumps of seaweed and sea-squirts disappear, leaving a featureless, undulating silt and mud substrate. Very occasionally, small groups of sea-squirts may be found on the substrate and Plate 2.3 shows one such example and the nature of the sediment at a depth of 9 metres. To the south, the loch shelves to a depth of 21 metres with no change in bottom type. This undulating mud plays host to occasional Carcinus, L. depurator, groups of Nephrops, and small fish including the goby, Lesueurigobius friesii which is often found inhabiting burrows produced by Nephrops.

Figure 2.3 Profile of shore at Eilean Mhartan along transect E.

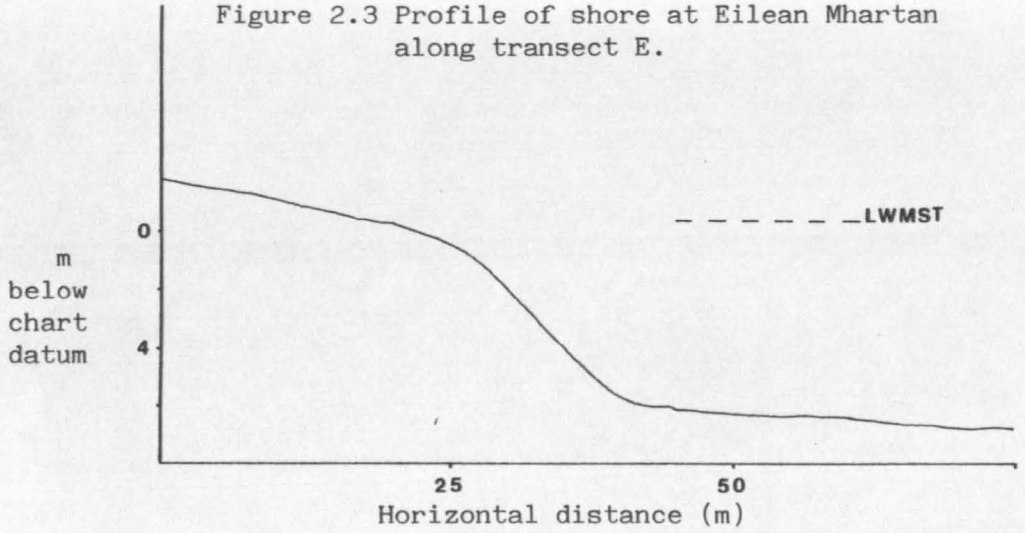
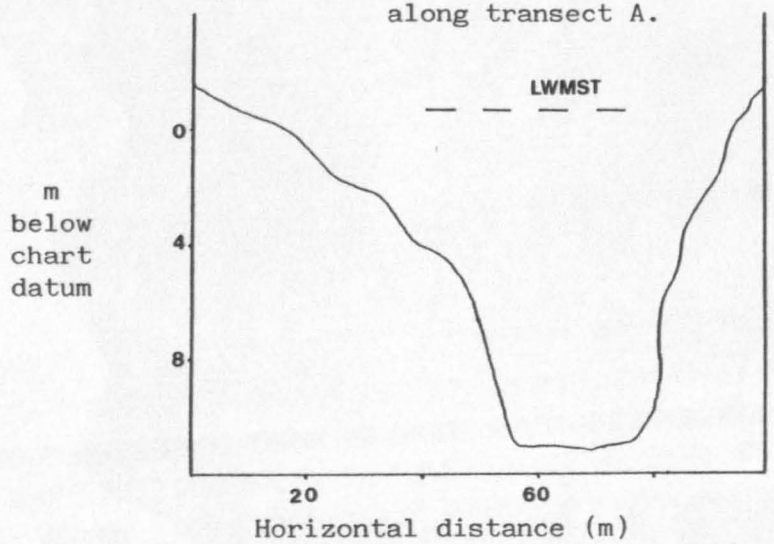


Figure 2.4 Shore profile at Port Lunna along transect A.



Shore profiles at Port Lunna

Figure 2.5

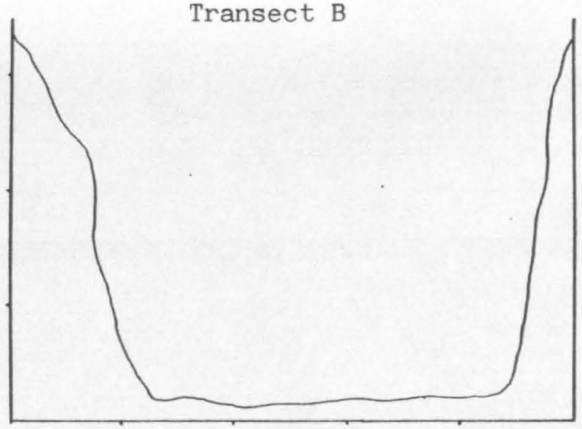


Figure 2.6

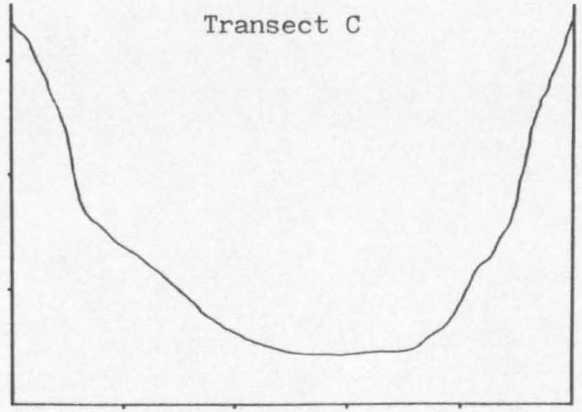
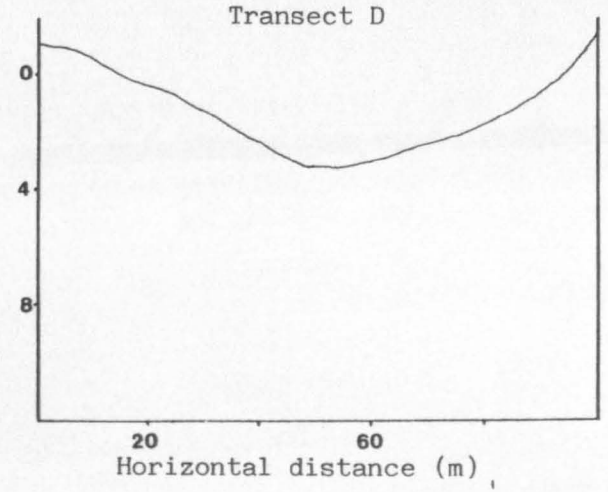


Figure 2.7



This site is not exposed to any noticeable tidal currents, and being surrounded on all sides by small hills, it is not troubled by adverse surface conditions, except in the most extreme circumstances. This enabled diving work to be carried out throughout the year.

PORT LUNNA

Port Lunna is situated only 1200 metres due west of Eilean Mhartan, but the two sites differ quite markedly in some of their features. Port Lunna is a steep sided inlet almost 500 metres long. The mouth of the inlet faces south west and is almost 100 metres wide. Sub-littorally however, this opening is restricted by rocky outcrops on either side. Figure 2.4 shows the profile at the mouth of Port Lunna along transect A (Figure 2.2). The centre channel reaches a depth of 12 metres but is restricted in width to approximately 30 metres by the rocky outcrops. This constriction results in Port Lunna forming a reasonably enclosed system. To the north of this constriction, vertical rock faces drop from the surface to a depth of 11 metres where they give way to a fine silt and mud substrate identical to that at Eilean Mhartan (Plate2.4). Figure 2.5 shows the underwater profile along the transect line B (Figure 2.2). The rock faces at this point are sheer and have few crevices or breaks in which animals may shelter. Further up the inlet (Transect C, figure 2.2), the vertical underwater rock faces drop to 6 metres and from 6 metres to 11 metres the walls take the form of an underwater scree slope (Figure 2.6). The boulders forming this scree slope are variable in size but many are as large as 6-7 feet in diameter. From this point to the head of the loch, the rock faces are covered in large cracks and

fissures. These provide valuable cover and protection for a number of species, including L. depurator (Plate 2.5). The rock faces and scree slope are covered in thick weed and bryozoan and hydroid mats, (Plate 2.6) and this plus the large gaps and crevices between the boulders provides a very diverse habitat. In the shallow water at the head of the loch, no rock faces or boulder slopes exist; instead, the bottom is a shallow shelving sand substrate (Transect D, Figure 2.7). Prevailing south westerly winds have resulted in thick mats of kelp in this region, again providing ample cover for a great many species. Port Lunna, therefore, provides considerably more cover and a more diverse habitat than does Eilean Mhartan. In addition, the enclosed nature and more varied habitat of Port Lunna might result in greater competition for resources and might also act as a feeding sink for the seals and dogfish known to exist there. These differences in the sites and their close spatial association therefore make the area ideal for comparison between different populations. This kind of approach may provide an insight into a possible range of natural behaviour, and possible differences in levels and type of aggression due to different competition and predation pressures.

However, access to Port Lunna is not possible by road and a boat is essential to enable study at this site. Unfortunately a boat was not readily available and consequently study at port Lunna was severely restricted compared with that at Eilean Mhartan. Due to this limited period for comparison, the rationale for studying two sites was simply to increase sample size and to check the generality of results.

2-2.2 OBSERVATION AND RECORDING TECHNIQUES

Regular field observations using SCUBA techniques were made at Eilean Mhartan between February 1981 and June 1982 and at Port Lunna between April and June 1982. During this period, 217 man dives were carried out resulting in almost 163 hours of total underwater time. Prior to April 1982 regular observations at Port Lunna were impossible due to unavailability of a boat.

For practical reasons, diving was generally carried out at approximately mid-day although on occasions a number of dives were made at different times during one day to investigate the possibility that abundance and distribution of crabs varied with time of day. No such variation was observed. Diving was always carried out in pairs and on entering the water, divers swam abreast, 1 metre apart along predefined paths. Diving always commenced at the same spot and an approximately identical path was followed on each dive with divers employing compass directions and distance estimation to gauge their position. On subsequent dives, permanent features on the seabed were used as markers to ensure the same area was covered. The dive starting points were picked for their convenience to the shore and the route predefined to ensure completion of the dive within easy reach of the shore. At Eilean Mhartan an area of approximately 300 m^2 was covered while an area of approximately 250 m^2 was covered at Port Lunna. The substrate was scanned within limits of visibility for swimming crabs. Clumps of sea-squirts, seaweed fronds or other obstructions were removed to prevent crabs remaining undetected. On encountering a crab behavioural observations were made for a short period of time before its capture. This observation period

varied according to the activity of a particular individual. Crabs in the process of escaping were captured immediately, as were crabs which were buried or semi-buried in the substrate. Crabs involved in any form of intra-specific interaction were left undisturbed as long as possible, and the behaviour patterns recorded. All recording was by pencil on formica slates.

After capture, each crab was tagged and the following information recorded before release.

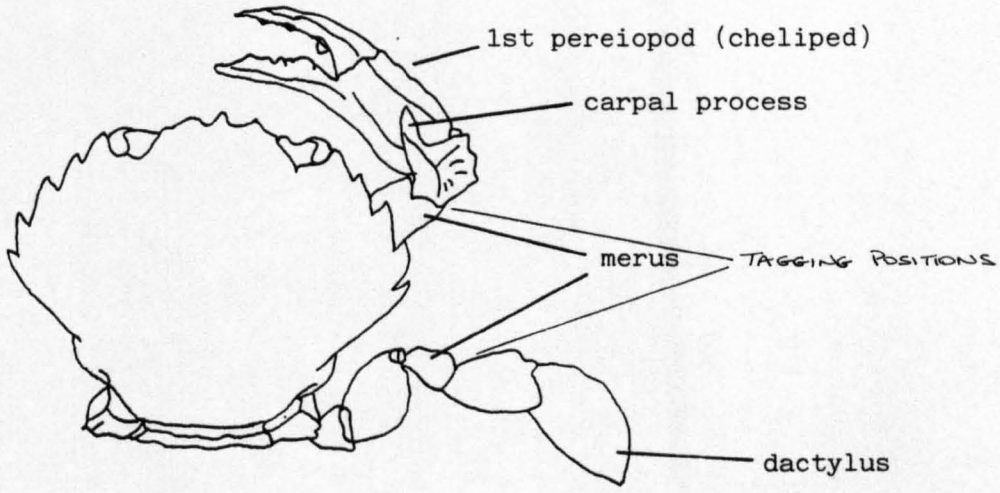
1. Carapace width. Width in mm between the 5th antero-lateral teeth (Figure 2.8)

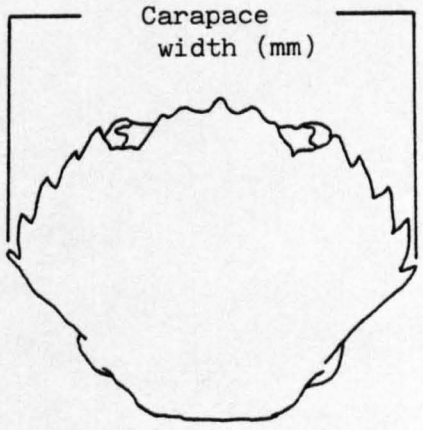
2. Sex. Individuals were classed as being male, female or juvenile ≤(20 mm). No attempt was made to determine the sex or to handle crabs smaller than 20 mm carapace width. Crabs of this size may easily have been damaged by handling. In addition, processing crabs of this size would have been extremely difficult while wearing thick diving gloves.

3. Limb complement. The absence, or reduced size, of any limb was noted. Missing limbs result from an autotomy reflex set up when a limb is grasped or badly damaged. Missing limbs were therefore taken as an indication of involvement in aggressive encounters. This may have been either inter or intraspecific aggression.

4. Position of crab in relation to available cover, and position in substrate when first sighted. The following categories were used.

Figure 2.8





Outline of L. depurator showing tagging positions and definition of width measurement. TERMINOLOGY FROM INGLE (1980)

a) Crabs associated with cover.

   i) On top of weed

   ii) Underneath weed

   iii) Under cover other than seaweed

b) Crabs found in exposed areas

   i) Standing on exposed mud/silt substrate

   ii) Sitting on exposed mud/silt substrate.

   iii) Semi-buried in exposed mud/silt substrate.

   iv) Totally buried in mud/silt substrate in exposed area.

c) Crabs standing on stone or boulder substrate.

5. Distance (metres) from previously processed crab. Distances between crabs were estimated and no attempt was made to measure this rigidly. Such an approach would have been impractical in the field particularly when dealing with highly mobile animamls. Distance estimation was simple in cases where more than one crab was in the field of view and when distances were small, but more complex when distances between successive animals were great. In the latter case, the number of fin strokes needed to move the diver from one crab to the next was taken as a guide to the actual distance. This is a standard navigation technique used by many divers.

6. Individual identification. The number of the tag placed on the animal.

All adult crabs were claw tagged using Cinch-Up Spaghetti tags purchased from Floy Tag and Manufacturing Inc., Seattle. Figure 2.9 shows one such tag with a four digit number printed on a yellow plastic collar. Tagging was carried out by passing the loop over a cheliped of the captive crab. The tag was then tightened around the merus posterior to the carpal process. Occasionally specimens without chelipeds were encountered. In these cases, the tag was placed aroung the merus of the fifth pereiopod (Figure 2.8). The carpal process of the cheliped or the flattened dactylus of the swimming leg prevented the tag slipping off or being actively removed. Juvenile crabs were not tagged due to difficulty in handling. In addition, the rapid moult rate of juvenile crabs would have rendered tagging useless.

Crabs were observed for a short period after tagging to investigate the possibility that tags affected the behaviour of the animals. In most cases the newly tagged animals pushed the dactylus of the first or second walking leg between the tag and the cheliped in an attempt to remove the tag. No crab was successful and this behaviour ceased rapidly. No other abnormal behaviour patterns were observed. Similarly, a number of tagged and untagged crabs were maintained in the laboratory and no behavioural differences were observed.

In the event of a number of crabs being encountered at one time during field studies, as many as possible were captured. Up to four crabs could be processed simultaneously by one pair of divers. In addition to the above information, evidence of food and feeding behaviour was obtained. Food items were removed from the mouth-parts or chelipeds of feeding crabs and identified as far as possible.

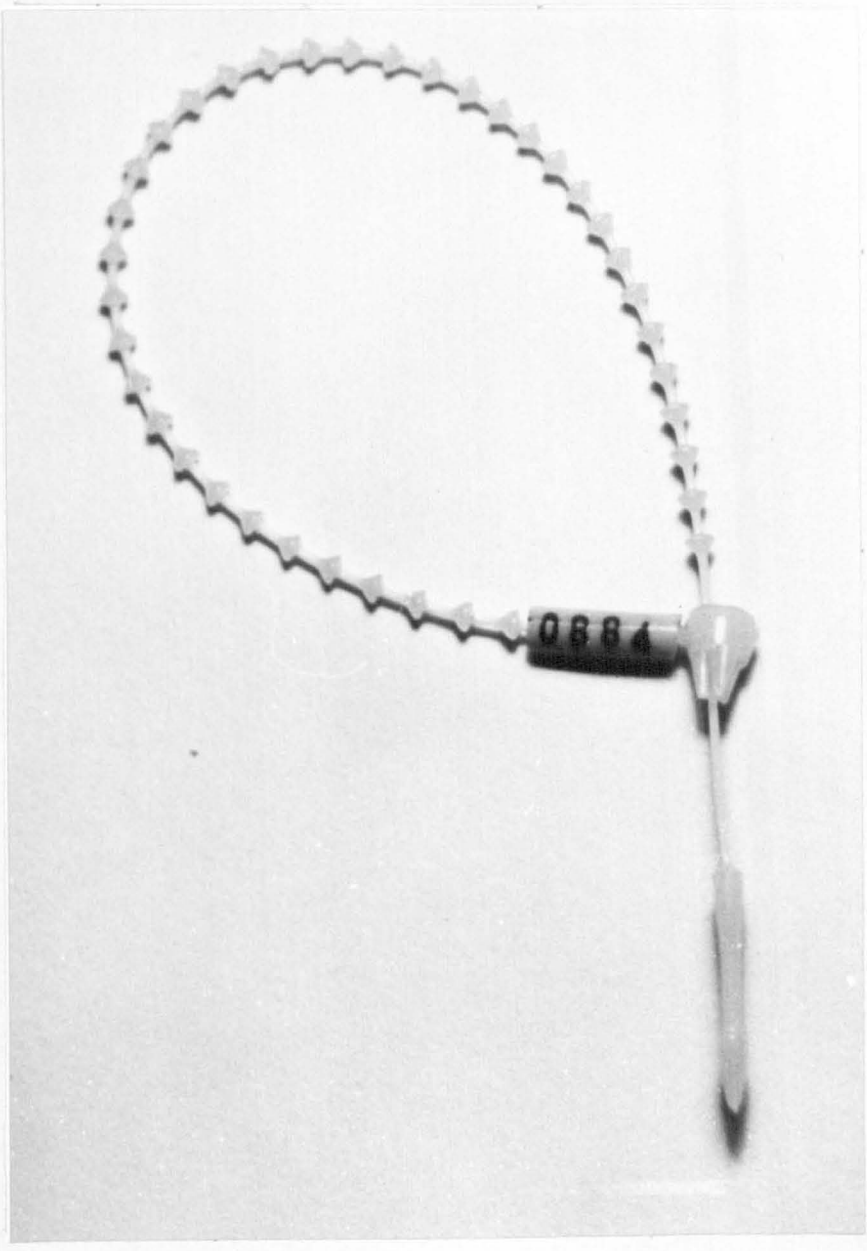


Figure 2·9

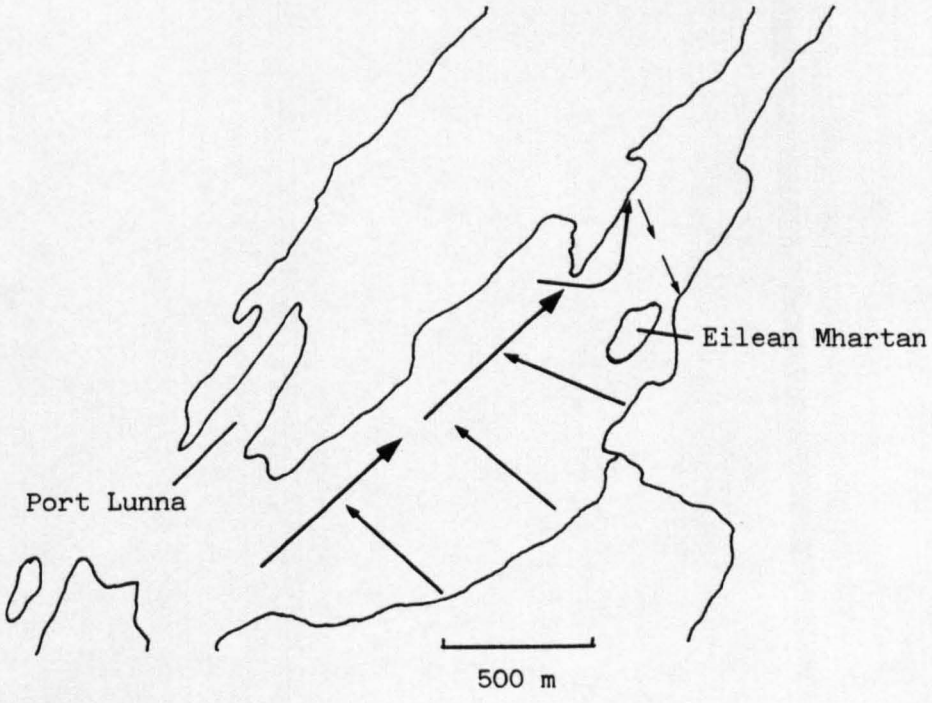
Photograph of Cinch-up Spaghetti Tag showing unique four digit number printed on plastic sleeve.

Each dive was terminated on completion of the predetermined dive path and on surfacing, tidal state, weather conditions, water temperature and estimates of underwater visibility were noted. On return to Glasgow all information was transferred to computer file.

In addition to the above, a number of major transect surveys were made in the area surrounding Eilean Mhartan in December, 1981 and March 1982. These were carried out in an attempt to identify migration of large numbers of crabs from the study site. The paths followed during these surveys (which were chosen to cover as much ground as possible) are shown in Figure 2.10, and involved pairs of divers swimming 1 metre abreast, along the predefined paths. As previously, the substrate was scanned and the position and distance between successive crabs was noted.

All dives were monitored from the surface and were carried out under Glasgow University and NERC Scientific Diver Regulations.

Figure 2.10 Map of Loch Sween showing paths covered during transect suryeys.



Represents path followed on individual transect.

Plate 2.1

Photograph showing substrate type at a depth of 4 metres at Eilean Mhartan. An adult male crab is shown standing on the pebble slope.

Plate 2.2

Photograph showing substrate type at a depth of 7 metres at Eilean Mhartan. An adult crab is shown sitting on a patch of weed and other debris.

Plate 2.3

Photograph showing the fine silt/mud substrate at a depth of 9 metres at Eilean Mhartan. A group of sea-squirts, rarely observed at this depth, are shown in the central area of the photograph.

Plate 2.4

Photograph of substrate type at a depth of 12 metres at Port Lunna. This substrate is identical in nature to that encountered at 9 metres (Plate 2.3) at Eilean Mhartan. This photograph also shows how well L. depurator blends into the background under natural light conditions.

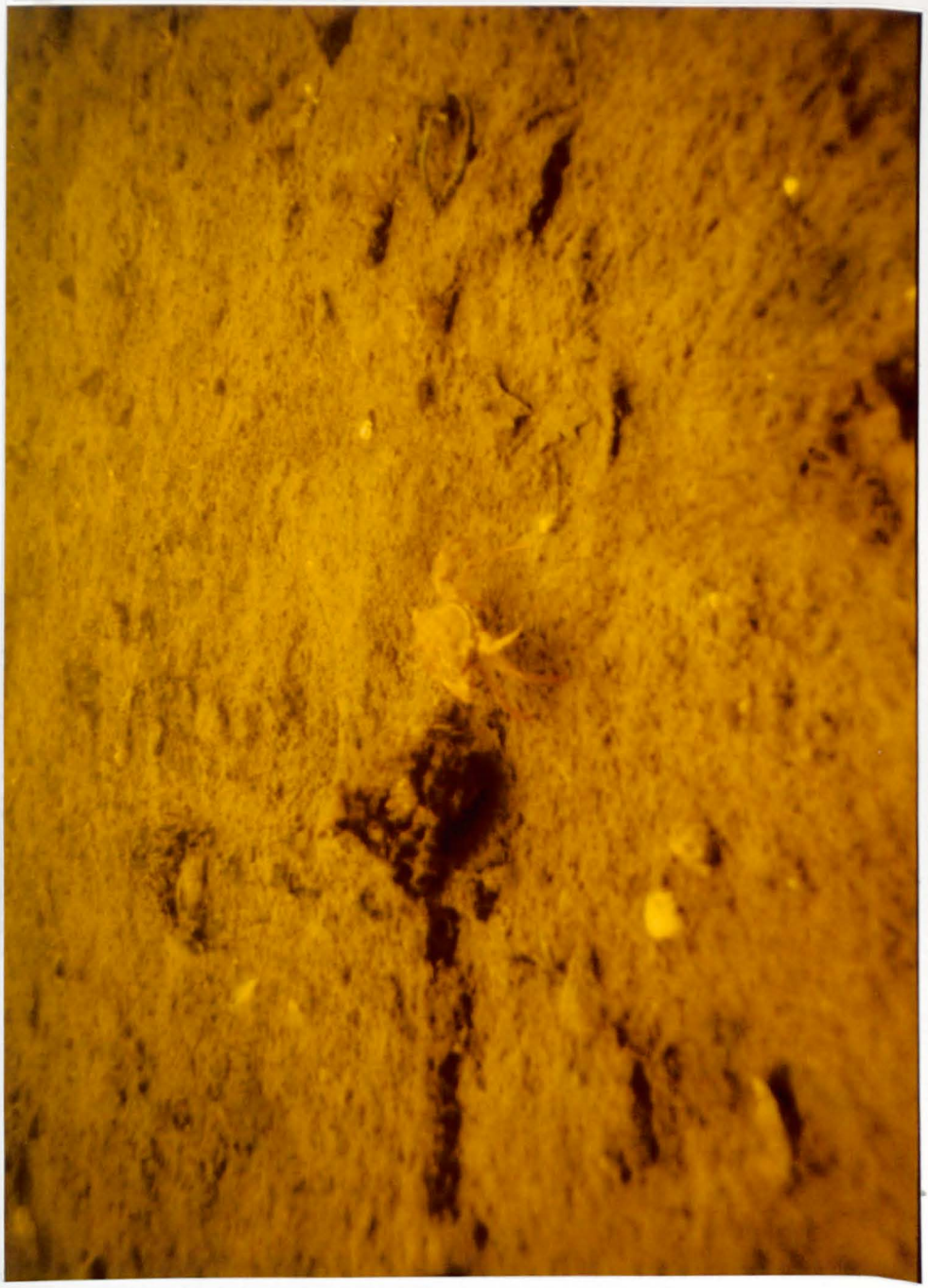


Plate 2.5

Photograph showing the nature of the vertical rock faces at a depth of 5 metres at Port Lunna (Transect C, Figure 2.2). Two adult swimming crabs are shown at the edge of a large crevice in the rock face. The rock surfaces are covered in an algal mat which in turn is covered in a thin layer of sediment.

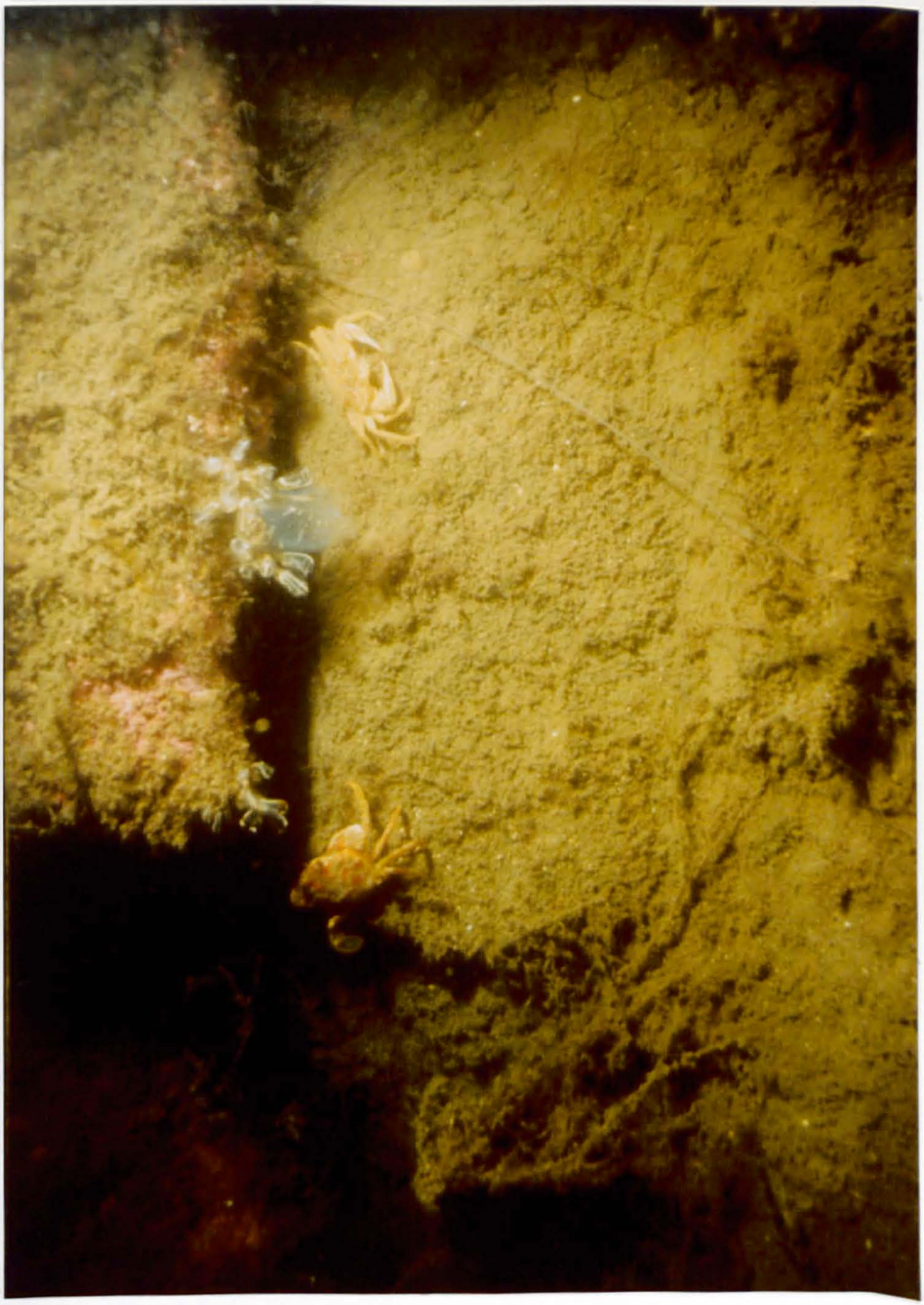
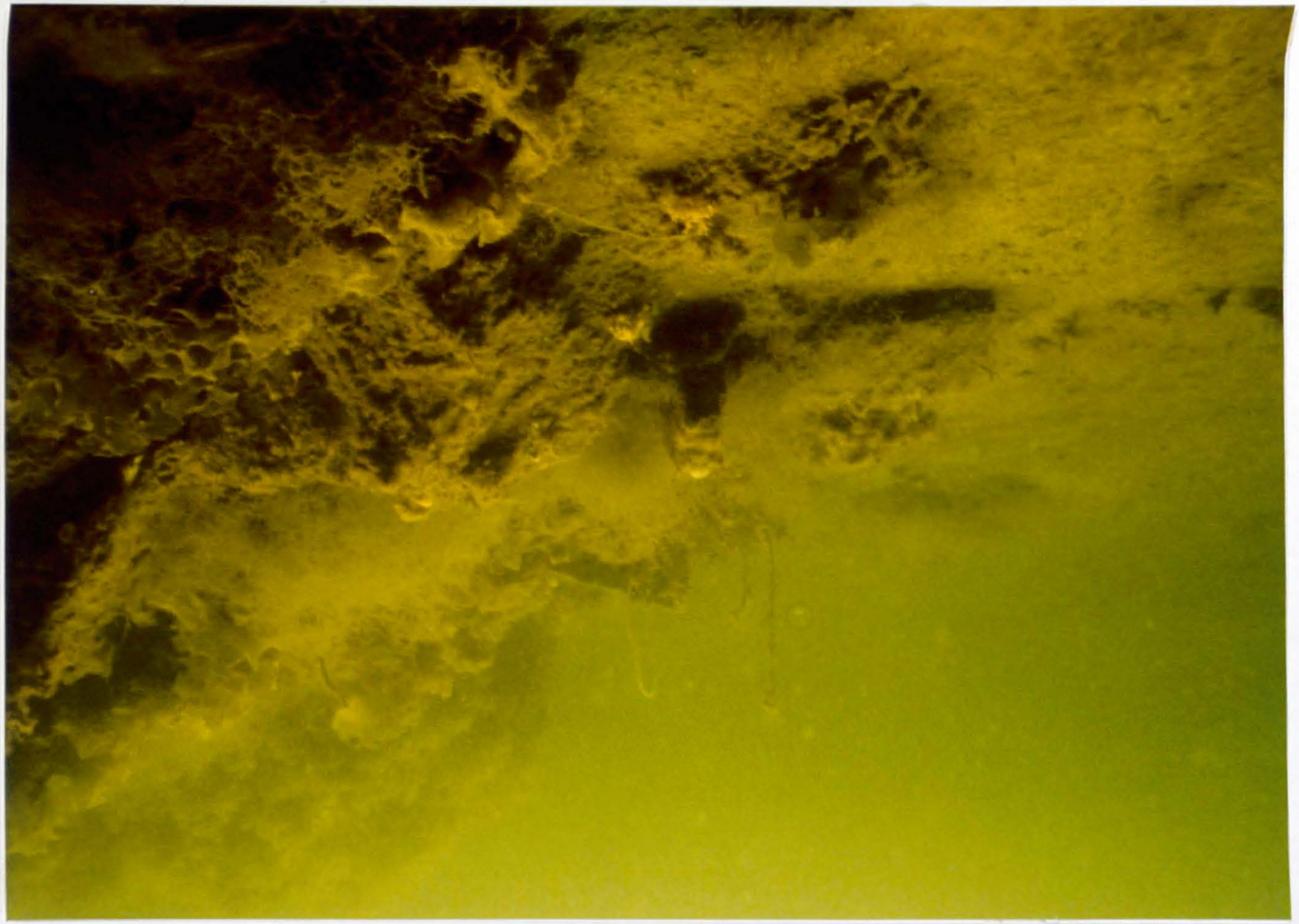


Plate 2.6

Photograph showing the base of the scree slope at a depth of 8 metres on the east side of Port Lunna (Transect C, Figure 2.2). The rocks and boulders are covered in thick weed and hydroid mats providing a diverse habitat and ample cover for L. depurator and other species

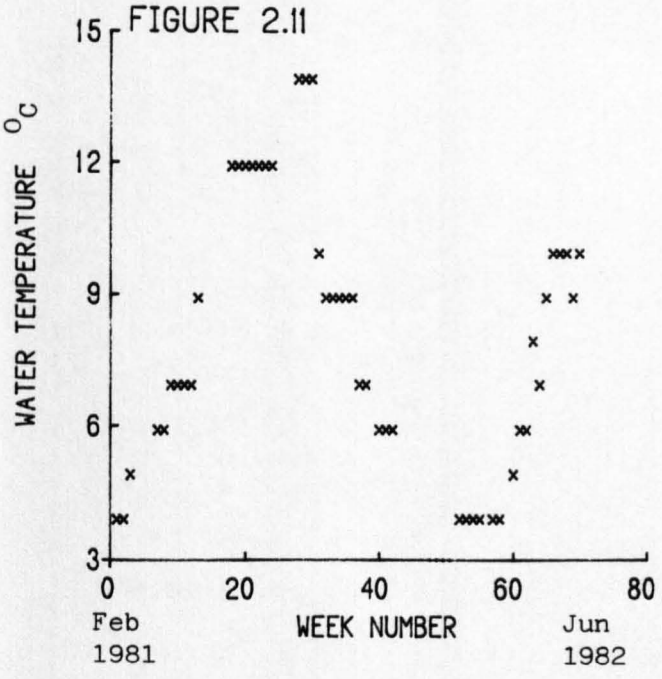


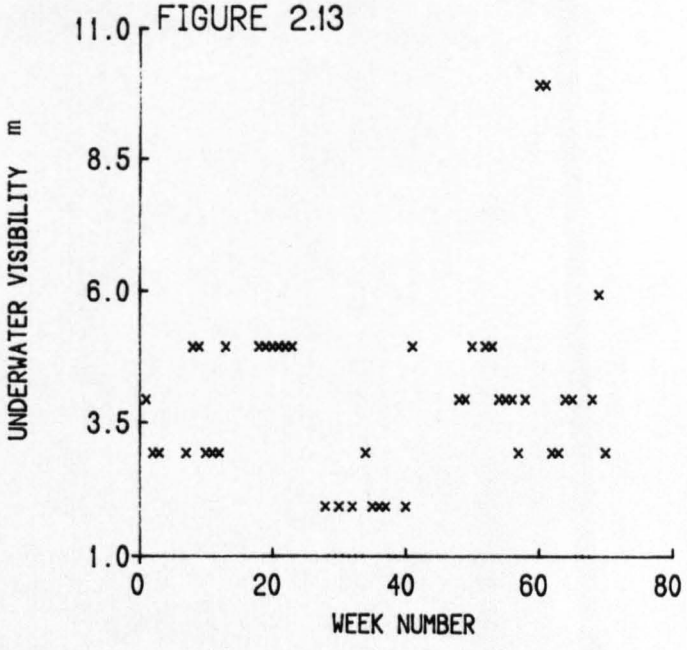
2-3 RESULTS AND DISCUSSION

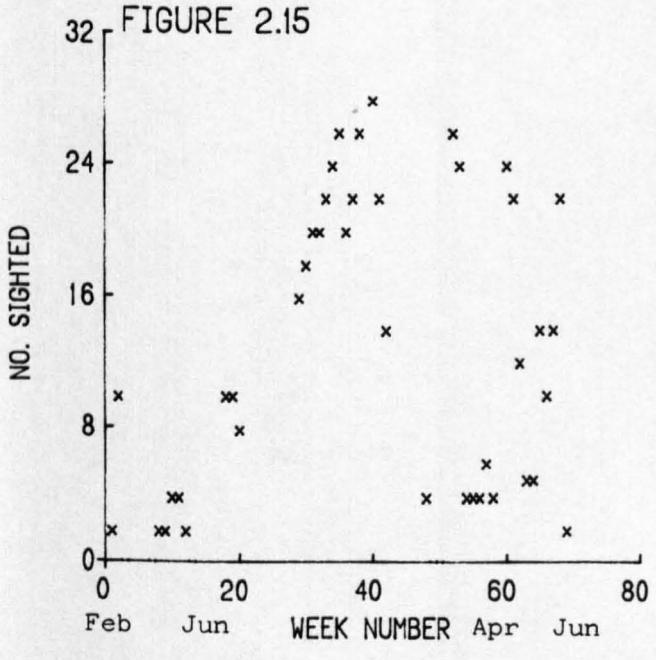
2-3.1 HYDROGRAPHIC CONDITIONS

Figure 2.11 shows the variation in water temperature at Eilean Mhartan for the period February, 1981 to June 1982. Temperature was highest between August and September with a maximum reading of 13°C at the sea-bed. The lowest temperature was recorded in December, January and February with the temperature remaining stable at 3°C. No diving work was attempted between 5th December 1981 and 15th January, 1982 due to severe weather conditions. Air temperature at Loch Sween over this period was recorded in the range 3°C down to -14°C and between 15th December, 1981 and 15th January, 1982 the sea around Eilean Mhartan was completely frozen over. These freezing air temperatures coupled with snow and ice rendered diving work impossible. Figure 2.12 shows water temperature at Port Lunna over the 12 week period during which field studies were carried out at that site. Water temperature was similar at both sites.

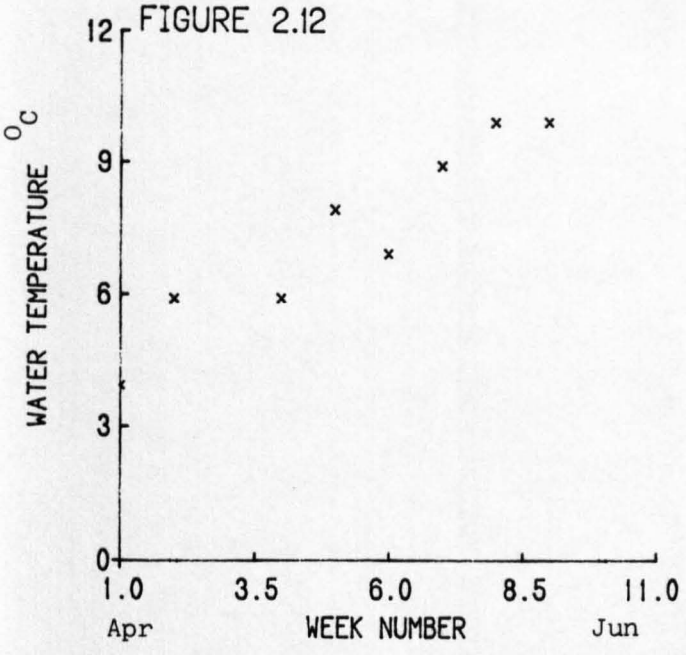
Numerous small rivers and streams flow into Loch Sween from the surrounding hills and during wet periods, this results in a surface layer of brown, peaty fresh water. This fresh water layer may reach a depth of 60 cm after prolonged wet weather and may change the quality of light penetrating to the sea-bed. However, both sites are well sheltered from the wind and sea conditions are generally calm. Consequently, little mixing occurs between the fresh water layer and the underlying sea water, thereby the full salinity of the sea water is

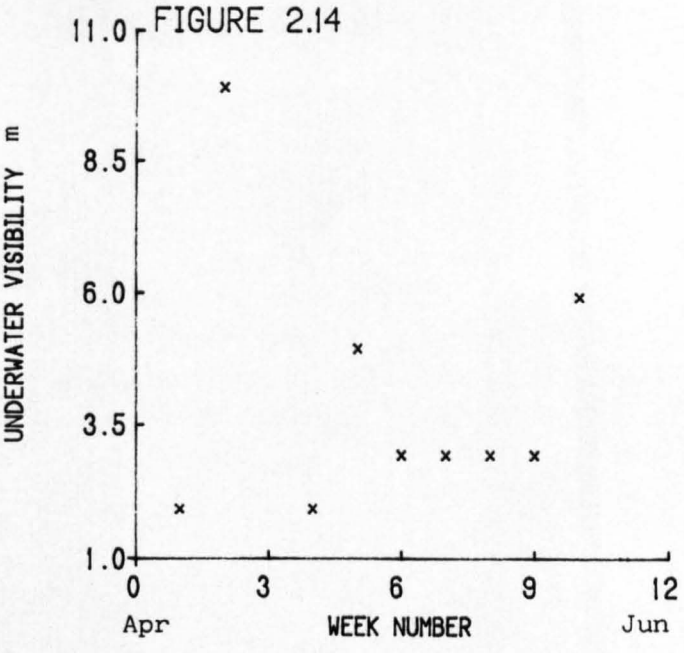


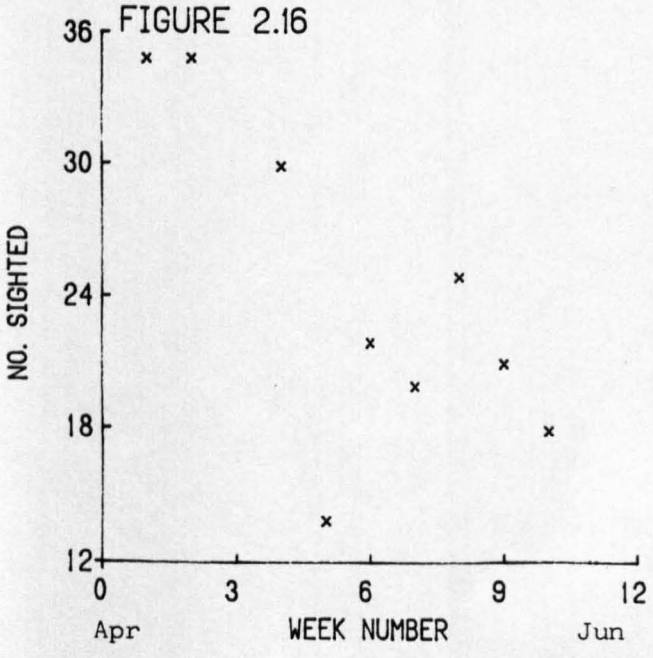




Variation in water temperature underwater visibility and number of crabs sighted at Eilean Mhartan for the period February 1981-June 1982.







Variation in water temperature underwater visibility and number of crabs sighted at Port Lunna for the period April 1982-June 1982.

maintained. Underwater, horizontal visibility was constantly poor over the study period, rarely rising above 5 metres (Figures 2.13 and 2.14) at either site. This was due to the nature of the sediment which, if disturbed, remained in suspension for some time before settling out.

The enclosed nature of Port Lunna might have been expected to produce different temperature, salinity or turbidity conditions. This was shown not to be the case with similar hydrographic conditions being evident in the two study areas. This result is not surprising for two such closely related sites.

2-3.2 ABUNDANCE AND POPULATION STRUCTURE

Figure 2.15 shows the number of crabs sighted per dive at Eilean Mhartan. Fewer than 10 crabs per dive were observed between February, 1981 and August, 1981 corresponding to a density of less than one crab/30 m^2 while up to 30 crabs per dive were sighted in the period September, 1981 to November, 1981. Subsequently, numbers fluctuated widely between 0-26 crabs per dive. Similar results obtained from the restricted sampling period at Port Lunna are shown in Figure 2.16. Average values over the sampling period at each of the sites were 1 crab/25 m^2 and 1 crab/10 m^2 at Eilean Mhartan and Port Lunna respectively. These average density values are not comparable as the restricted sampling period at Port Lunna (carried out during peak abundance) will bias towards higher density. In periods of peak abundance, the overall density of crabs at Eilean Mhartan was 1 crab/10 m^2 while a slightly higher figure of 1 crab/7

m^2 was obtained at Port Lunna. The more varied habitat at Port Lunna offers more cover to crabs than does Eilean Mhartan (see section 2-3.3) and this may in part explain the higher density observed at Port Lunna. The values for overall population density calculated at time of peak abundance are relatively low compared with the results on the rock crab Cancer irroratus (Drummond-Davis, et al, 1982) and the shore crab Carcinus (Dare and Edwards, 1981) where densities of $1/m^2$ and $1.8\text{-}2.5/m^2$ respectively were recorded. Dare and Edwards (1982) also suggested that the true density of Carcinus may be as high as $2.0\text{-}2.5/m^2$ if allowance was made for experimental technique. However, in a detailed study of Nephrops in a small area of sea-bed, Chapman and Rice (1971) reported a density of $1/8m^2$, a value comparable to that reported for L. depurator in this study.

Comparison of Figures 2.15 and 2.11 indicates that variability in numbers of crabs observed at Eilean Mhartan may be related to temperature with peak abundance occurring during periods of high water temperature. Figure 2.17 indicates that there is a significant relationship between number of animals sighted and water temperature ($F = 16.52$, $n = 42$, $p < 0.05$). However, there is no relationship between number of animals sighted and underwater visibility (Figure 2.18; $F = 0.57$; $n = 42$; $p > 0.05$) suggesting that sampling efficiency was not affected by poor underwater visibility. These results suggest that while the number of crabs at Eilean Mhartan fluctuate widely, there is a relationship between the number of crabs sighted and temperature, with more crabs being observed during periods of warm water. On the other hand, localised variability in underwater visibility did not appear to be responsible

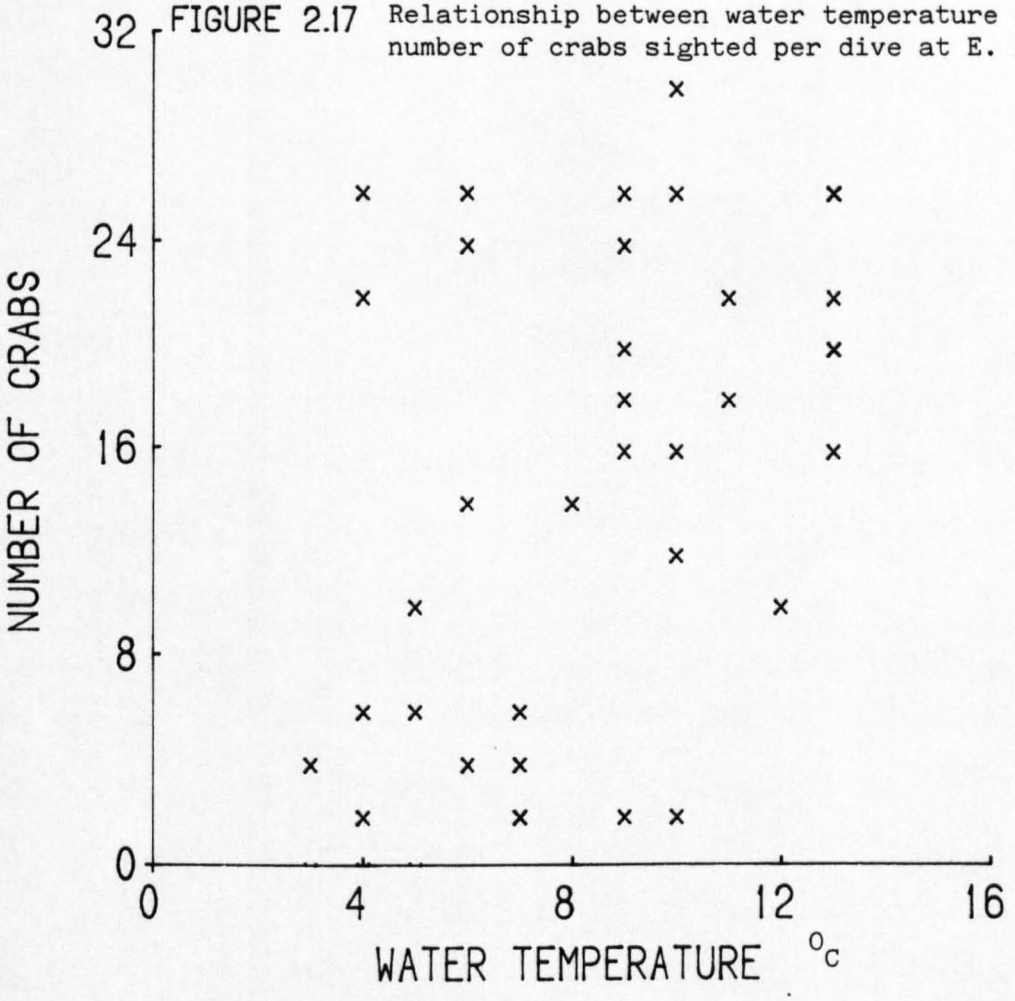


FIGURE 2.17 Relationship between water temperature and number of crabs sighted per dive at E. Mhartan.

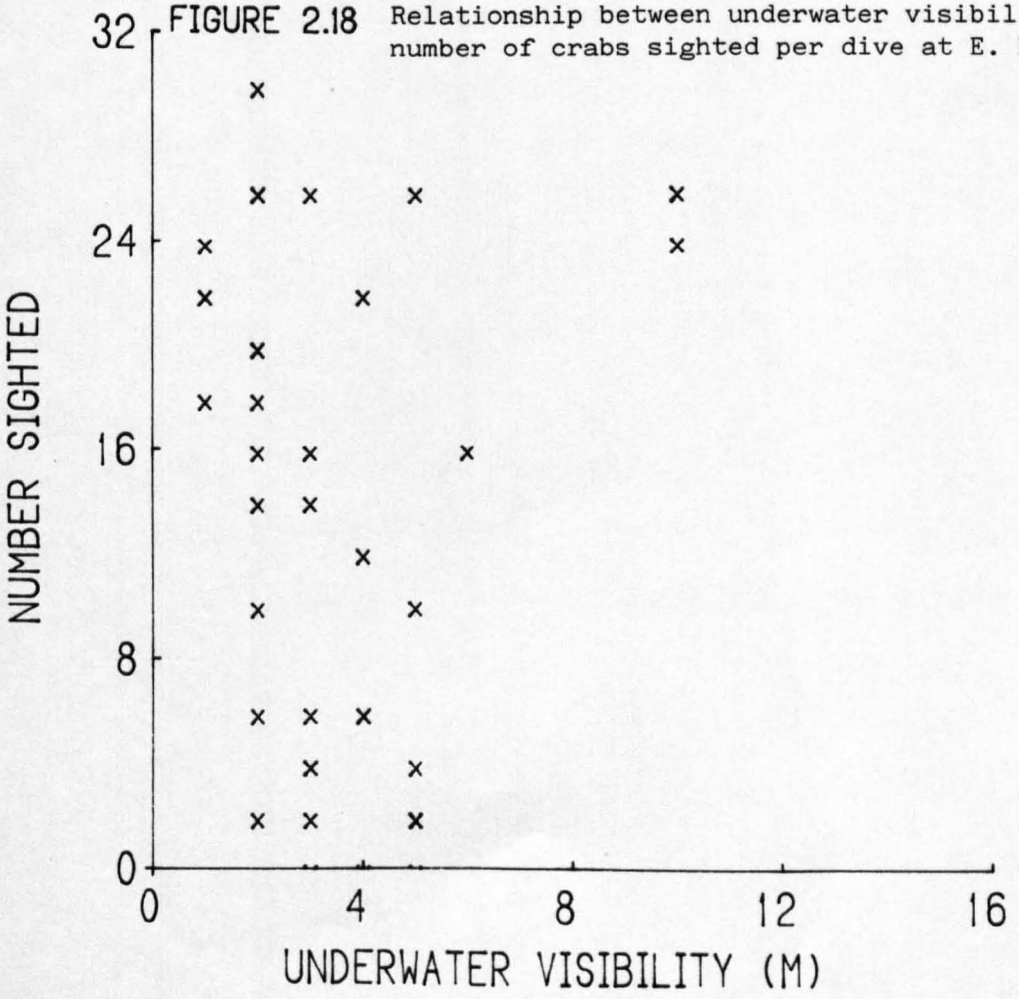


FIGURE 2.18 Relationship between underwater visibility and number of crabs sighted per dive at E. Mhartan.

for the fluctuations observed. The nature of the relationship between abundance and water temperature is not clear and further work is required to see if the relationship is causal or merely coincidental.

Figure 2.19 presents data for adult crabs (> 20 mm) at Eilean Mhartan and a much clearer trend appears. The corresponding data for juvenile crabs is shown in Figure 2.20 and is discussed later. Few adult crabs were observed at Eilean Mhartan between February and August 1981. Peak abundance was reached in September and October before a rapid decline over the winter months. Numbers remained relatively stable between December 1981 and April 1982 before increasing again, presumably to a peak in September and October. Too few data were obtained from Port Lunna for any detailed comparison to be made; however, numbers at both sites (Figures 2.19 and 2.21) were similar during the period when joint sampling was carried out. Figure 2.19 shows a rapid decline in abundance of adult crabs between November 1981 and January 1982. This suggests that, either crabs are being removed from the local population by death/ predation or that there is large scale movement away from the area. It is unlikely that the decline in abundance resulted directly from increased predation as no obvious increase in predators was observed at the period in question. In addition, increased predation would almost certainly have resulted in an increased incidence of mutilation and possibly incidence of undigested tags in the study area. No such observations were made. Therefore, the most likely explanation for the decrease in abundance is that of movement away from the area.

Examination of Figure 2.19 also reveals differences in the sex ratio at Eilean Mhartan. More males than females were observed during

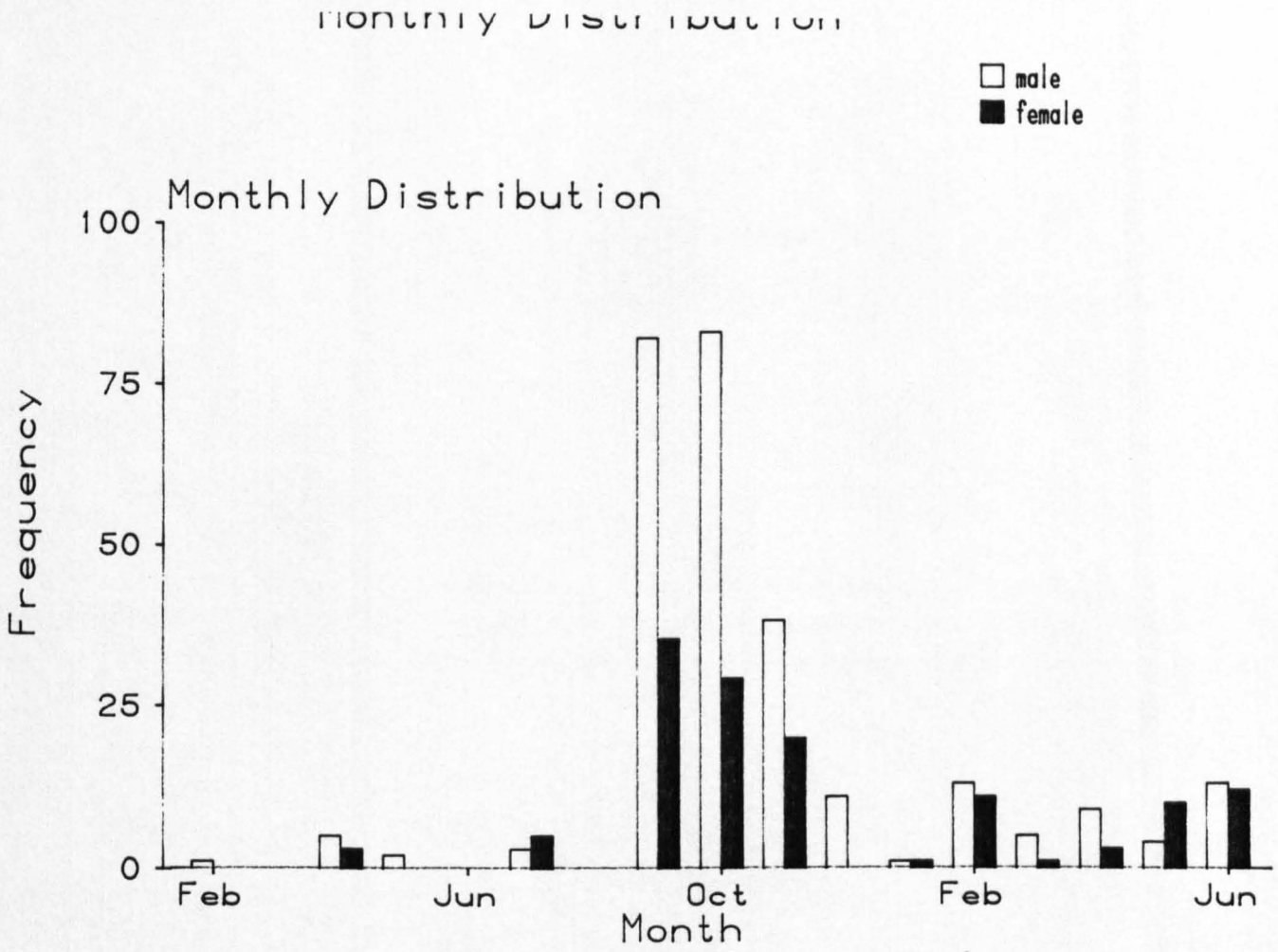


Figure 2.19 Monthly distribution of L. depurator larger than 20mm width at Eilean Mhartan.

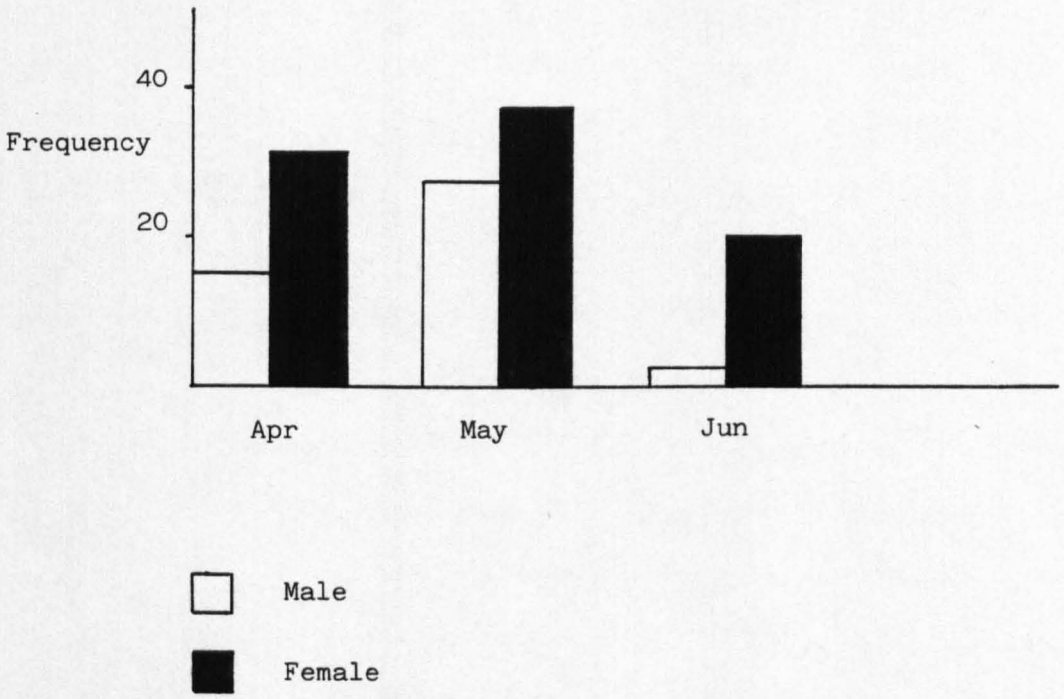


Figure 2.21 Monthly distribution of adult crabs (>20mm) at Port Lunna.

the period September-December (Table 2.1) although the sex ratio was not significantly different from 50:50 during all other periods of the study. These observations suggest differential movement to and from the study site resulting in a sex ratio biased in favour of male crabs. Sex biased migrations are common in decapods (Allen, 1966) and may be related to the breeding cycle. Cancer pagurus females are much more mobile than male crabs (Bennet and Brown, 1983) and the offshore migrations of the females seem to be related to the breeding behaviour, ensuring a suitable sea-bed substrate for berried crabs and/or allowing distribution of the larval phase under suitable current conditions. A similar migration pattern has been reported for the commercially important swimming crab Callinectes sapidus (Cargo, 1959; Williams, 1965; Tagatz, 1968; Perry, 1975) whose females migrate from estuaries to the sea where the eggs hatch. Similarly, seasonal differential distributions of males and females have previously been reported for the swimming crabs Callinectes arcuatus, Callinectes toxotes (Norse and Esterez, 1977) and Callinectes maracaiboensis (Norse, 1977).

In an attempt to identify any such differential or mass migration from the study site in the current study, transect surveys (see section 2-2.2) were undertaken. No swimming crabs were observed on any of these transects. This implies that if large scale movement away from Eilean Mhartan was occurring, the movement was swift and resulted in crabs moving completely out of this area of Loch Sween, a distance of at least 1500 metres. In a recent study on th edible crab C. pagurus (Bennett and Brown, 1983) migrations of up to 114 km were reported, while for migrant American lobsters (H. americanus) Uzmann et at (1977) reported an average speed of travel of 1.8 km

Table 2.1 Showing sex ratio at Eilean Mhartan over the period September-December 1981.

Month	Number of male crabs	Number of female crabs	X^2	
September	82	35	18.08	$p<0.001$
October	83	29	25.08	$p<0.001$
November	38	20	16.05	$p<0.001$
December 1981	11	0	9.09	$p<0.01$

per day, with a maximum speed of 11 km per day. Certain crustaceans are therefore capable of undertaking long and rapid migrations. L. depurator is considerably more agile that either C. pagurus or H. americanus and is capable of travelling at much greater velocities. It is therefore possible that individuals were capable of moving rapidly from the study site. Nevertheless, it is unlikely that a large population of adult swimming crabs could have carried out such a migration without detection of some individuals on the extensive transect surveys. Other possible explanations for the observed decrease in population are that individuals were hiding locally or that predation increased in response to increase in abundance of adult crabs.

The study area and area covered during transect surveys was carefully searched on each dive and all obstructions or possible cover were raised or displaced in order to detect hidden crabs. It is inevitable, despite the care taken, that some crabs remained undetected during these searches. Nevertheless, it is extremely unlikely that this could account for all of the observed population fluctuations. On the other hand, while there was little visible evidence of increased predation during periods of peak abundance, this peak abundance did coincide with warmer water temperatures and increased numbers of fish such as goldsinny wrasse (Centrolabrus rupestris). It is therefore possible that predation was higher during periods of warmer water; however, the most plausible explanation for the observed decline is a combination of increased predation and migration away from the site in question. Further work is obviously required in order to determine the true nature of the phenomenon.

SITE ATTACHMENT

Crabs at both sites were individually tagged in an attempt to investigate the stability of local populations and to obtain some information concerning long term site attachment by individuals. A total of 279 adult crabs were claw tagged and released at Eilean Mhartan. Fifty six of these (20%) were resighted in the study area on at least one subsequent occasion. This value compares favourably with the results of nine other studies on Nephrops where the maximum recapture value was 14.7%, and in most cases was much lower (<1%) (Chapman, 1980).

Figure 2.22 shows sighting data for those crabs observed more than once and includes the date of tagging and each subsequent sighting of an individual. Crabs which were tagged and never re-sighted are not included. The large number of crabs tagged in September 1981 and subsequently re-sighted, reflects the large increase in population at this time an does not reflect increased sampling effort. Figure 2.23 shows elapsed time between tagging and final sighting of individuals. Of the 56 crabs resighted after tagging, 25 (45%) were observed on one occasion only, one week after tagging. One male crab was observed 20 weeks after tagging and one female was resighted after a period of 23 weeks. 175 male and 104 female crabs were tagged while 42 male and 14 female crabs were resighted on at least one occasion. There is no significant difference between the number of male crabs resighted and female crabs resighted (X^2 = 3.7, 1 d.f., $p > 0.05$)

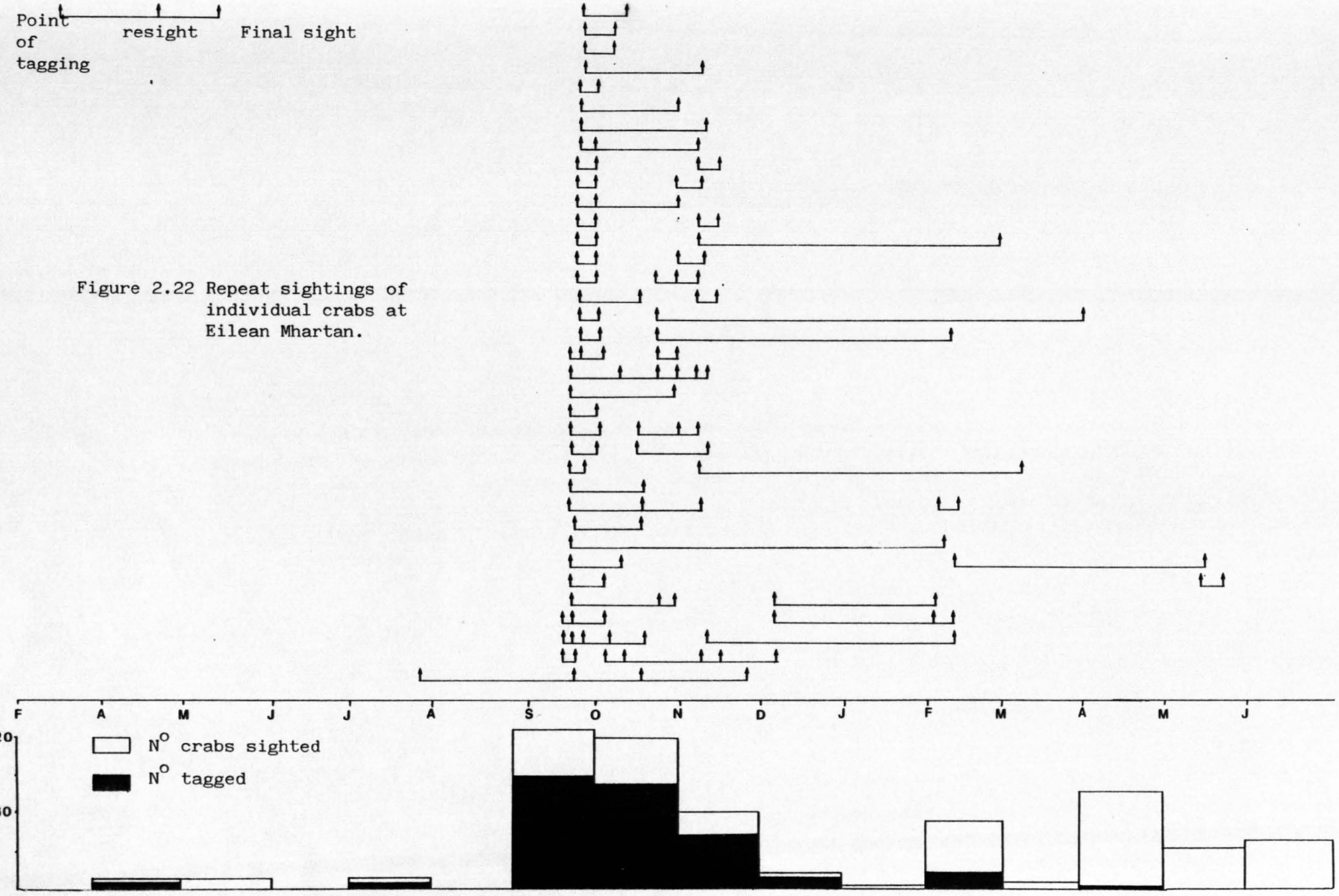
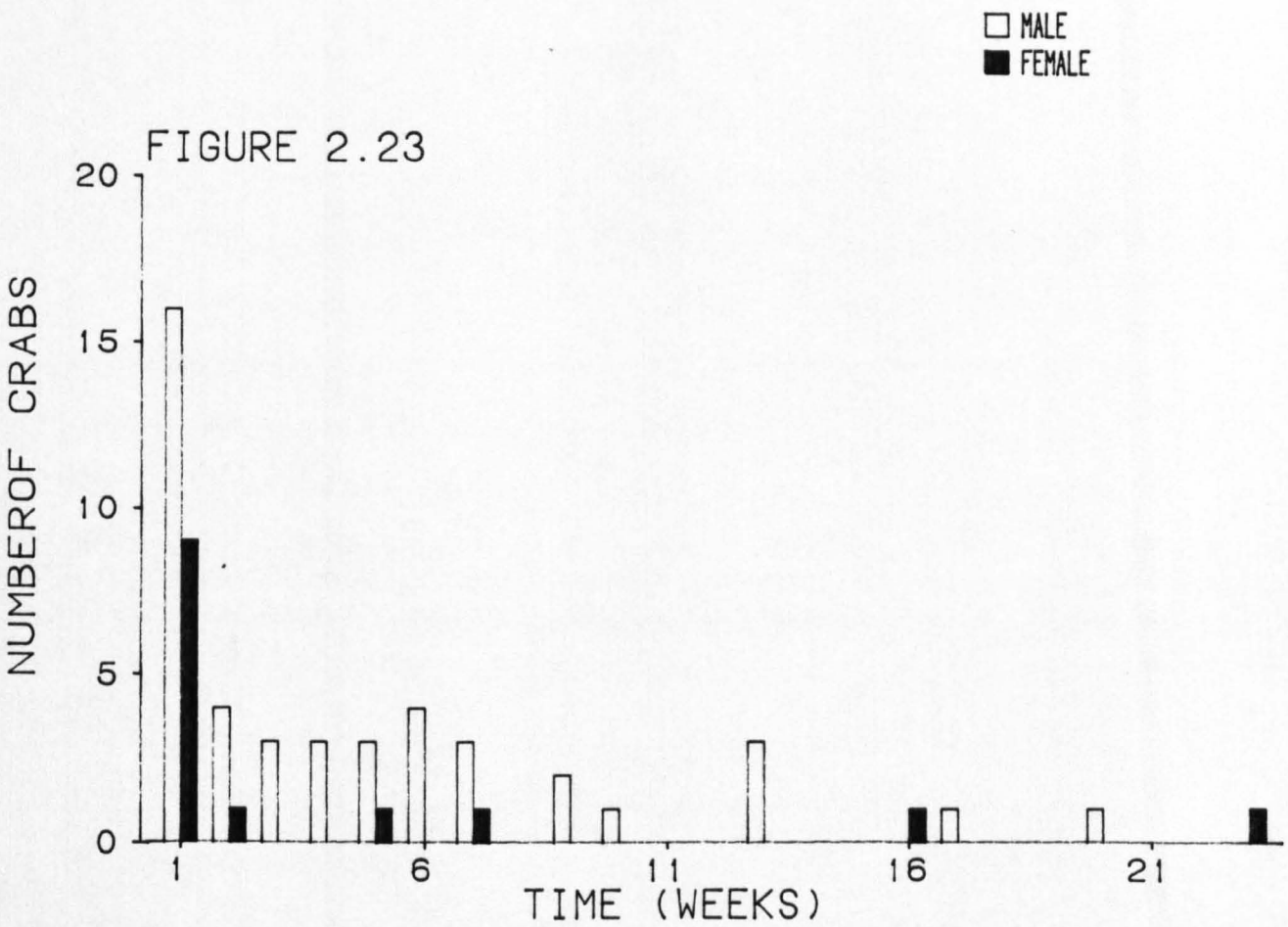


Figure 2.22 Repeat sightings of individual crabs at Eilean Mhartan.

FIGURE 2.23



Relationship between time of tagging and final sighting of individual L. depurator at Eilean Mhartan.

X axis represents elapsed time (weeks) between tagging and the final resighting of an individual crab.

The fact that almost 80% (223 crabs, n = 279) of the tagged crabs were never resighted shows that individuals within the study area were continually changing even though in the short term the local abundance remained relatively constant. One possible explanation for this is that individual crabs managed to shed their tags and consequently appeared as newcomers to the area. However, on a number of occasions crab carcasses and moult cases still wearing tags were observed on the substrate. In addition, a number of unused tags were dropped in the study area and found 7 days later in the position in which they were dropped. Any tag shed by a crab in the area in question therefore would have been equally conspicious and readily observable by the divers. No such tags were found on the substrate suggesting that tag shedding was not a regular occurrence. The two tagged moult cases observed at Eilean Mhartan indicate that a small proportion of tags may be lost in this way, but additional support for longer term tag retention was provided by laboratory observations. Tagged individuals (15) (30 mm- 65 mm) were maintained under laboratory conditions for up to 3 months without an incidence of tag shedding or moulting. It seems likely therefore that tags were retained in the field for similar periods of time and some field observations (figure 2.23) back this up.

Other possible explanations for the disappearance of tagged individuals is that capture and tagging represents a traumatic experience which forces the animals to leave the area, or that conspicuousness of the tag increases the probability of predation. Any experimental manipulation of an animal will cause a certain amount of stress. Most crustacean tagging studies to date have involved tagging after capture by trawling or creeling. The possible

traumatic effects of this type of experimental manipulation have led workers to question the wisdom of using this approach and more recent studies have involved tagging underwater to minimise disturbance to the animals (Chapman, 1980). All animals in the present study were tagged underwater with as little disturbance as possible and while most crabs displayed an initial interest in the tag, this behaviour soon ceased and normal behaviour resumed. It seems unlikely therefore that the tagging experience resulted in mass migration from the study site.

The alternative possibility was that conspicuousness of the tag rendered an individual more prone to removal from the area by predation, thus allowing other individuals to take their place. Known predators in the area include dogfish, seals and other larger crustaceans (Carcinus and Cancer) (See section 2-3.5). It is unlikely that the possession of a tag should increase the possibility of capture by larger slower moving crustaceans but conceivable that it may result in more attention being shown by fish and seals. Little evidence of such increased predation exists, either in terms of mutilated specimens or undigested tags in the study area. Furthermore, the tags used were small and fitted neatly into the space between the carpus and merus (Figure 2.8) of the cheliped, thereby remaining inconspicuous to all but the closest scrutiny.

It appears, therefore, that the most plausible explanation for the observed decline in tagged individuals is a simple reflection of a fluid local population and is not induced by tagging or subsequent increased predation.

45% of resighting in the area occurred within one week of tagging. This suggests that some individuals may remain in the study area for a short period of time, implying a low level of temporal continuity within the sampled area. A smaller number of crabs were observed on a number of different occasions with certain individuals being observed up to 23 weeks after tagging (Figure 2.23). Initially this seems to suggest that a very low proportion (approximately 5%) show some form of long term site attachment. However, these animals did not remain in the study area (Figure 2.23) for the entire period between tagging and final sighting, but spent most of this time away from the area. All the evidence therefore indicates that L. depurator shows no site attachment and therefore is certainly not territorial at Eilean Mhartan and that while some individuals are responsible for a certain level of continuity, this is so low as to be of little significance.

While further work of this nature would be useful in order to obtain a clearer picture of the movements of individuals and populations of L. depurator the present study has nevertheless revealed similar patterns of migration and movement to those reported previously for Carcinus (Atkinson and Parsons, 1973). Seasonal migrations of Carcinus and movements of individual crabs within populations were described from the south of England (Edwards, 1958) and South Wales (Naylor, 1962; Crothers, 1968). These authors noted that most crabs overwintered in the shallow sublittoral region, migrating into the littoral zone in spring and from it in autumn. First year crabs and crabs in, or approaching terminal anecdysis tended to be non-migratory, the former remaining on shore and the latter offshore. Atkinson and Parsons (1973) also reported a marked onshore

migration in spring and migration offshore in late autumn for Carcinus. They also reported that most of the population took part in these migrations, with only the juvenile crabs tending to remain between the tidemarks in winter. Additionally, in spring male crabs migrated onshore before females, whereas in autumn both sexes left the shore at the same time, though there was some suggestion that the larger females moved offshore before the larger males. Fewer female than male Carcinus were present on the shore in all months of the year while during the summer months female crabs predominated in creels offshore indicating that a proportion of the female population was offshore. Edwards (1958) and Crothers (1968) also noted a preponderance of male crabs onshore in summer. However, for Carcinus this phenomenon appears to be localised as it has not been observed in other areas (Isle of Man) where in summer there is a 50:50 sex ratio in inshore collections and no predominance of females offshore.

In the current study a similar migration into the area was observed in late summer at Eilean Mhartan and out of the area in early winter. Unfortunately, attempts to examine the nature of this migration by transect surveys failed to yield any information. However, in light of the information available for Carcinus, it is possible that L. depurator also migrates onshore in spring and offshore in autumn. Further intensive diving surveys and tracking of individual crabs using ultrasonic tags would almost certainly elucidate the specific movement patterns shown by L. depurator in Loch Sween.

FINE SCALE DISTRIBUTION PATTERNS

The results presented above dealing with general population abundance and movement give little indication of distribution patterns of individuals within the study area. Figures 2.24 and 2.25 show frequency histograms of nearest neighbour distances obtained at both sites over the course of the study. At Eilean Mhartan 42% of the crabs observed were seen to be within 1 metre of the nearest conspecific, while at Port Lunna, 60% were within 1 metre of their nearest neighbour. Figure 2.26 shows that this trend exists throughout the course of the study and is not subject to seasonal variation. This suggests that in the areas in question, some clumping of individuals must occur and during periods of peak abundance, it was common to see up to five crabs standing within 0.5 metres of each other (personal observation). Tables 2.2 and 2.3 show examples from data files, of distance observed between five successive crabs at Eilean Mhartan, indicating clumping of individuals. These values for local density (3.3 crabs/m^2, table 2.2; 1.5 crabs/m^2, table 2.3) compare with the value of 2.0-2.5 suggested for Carcinus by Dare and Edwards (1981).

Figures 2.27 and 2.28 show this nearest neighbour distance (NND) information by sex for adult crabs. Again, it can be seen that the majority of crabs are to be found within 1 metre of each other irrespective of the sex of the nearest neighbour. The nearest neighbour distances obtained for each animal were calculated from estimates of the distance between successive crabs (see 2-2.2). Experimental error is inevitably induced by this approach and while estimates of distance were reckoned to be accurate to 1 metre, this

FIGURE 2.24 Frequency of nearest neighbour distance observed at Eilean Mhartan.

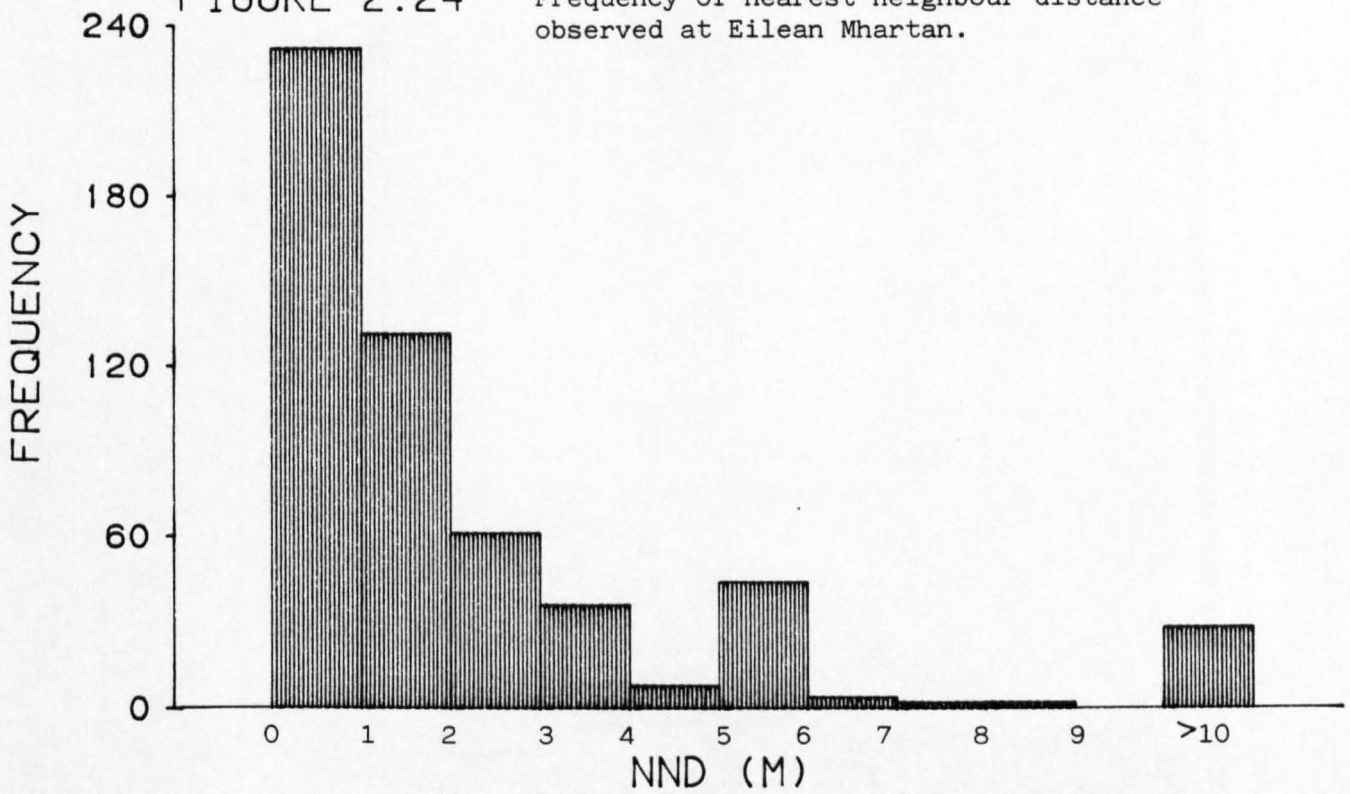
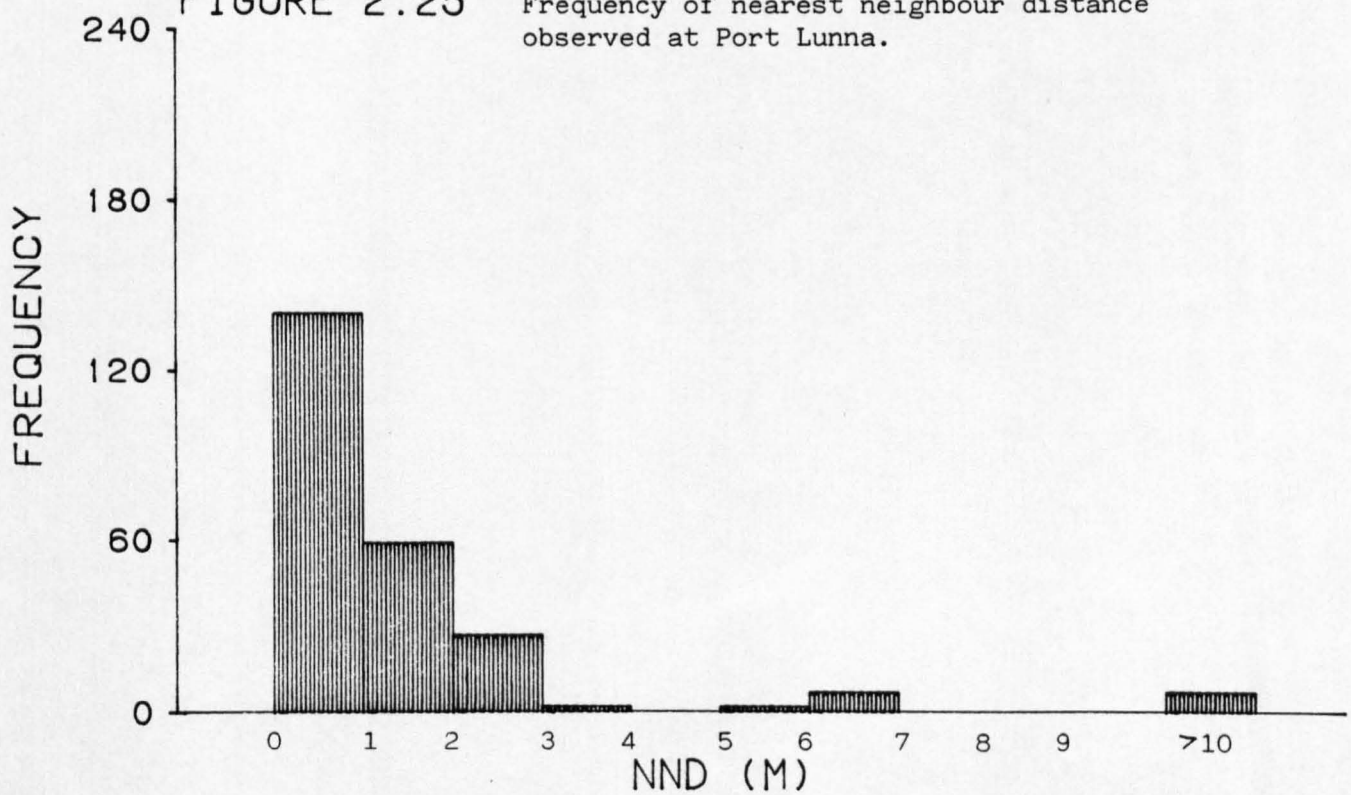


FIGURE 2.25 Frequency of nearest neighbour distance observed at Port Lunna.



MONTHLY NND DISTRIBUTION

Figure 2.26

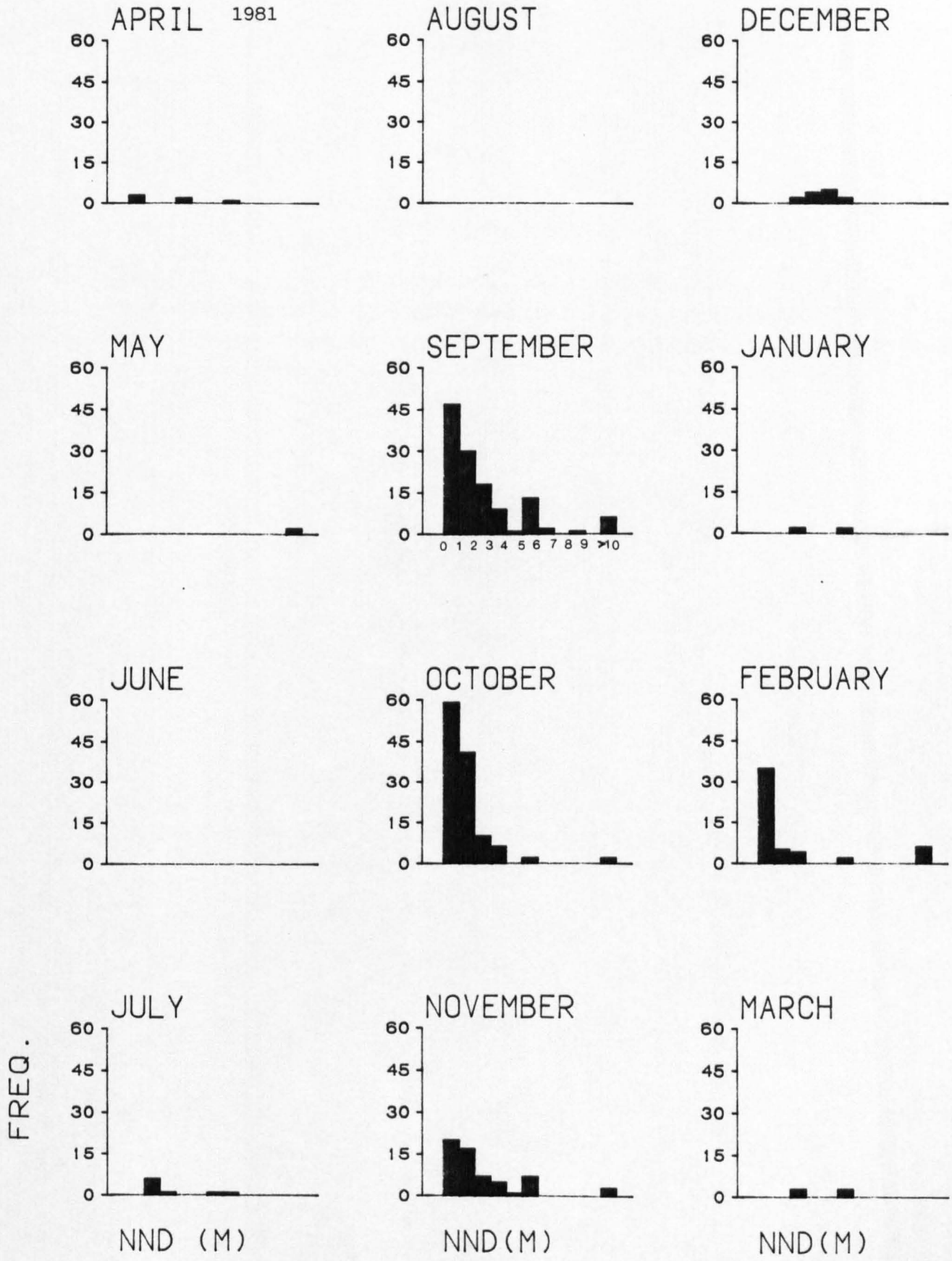


FIGURE 2.26 CONTD.

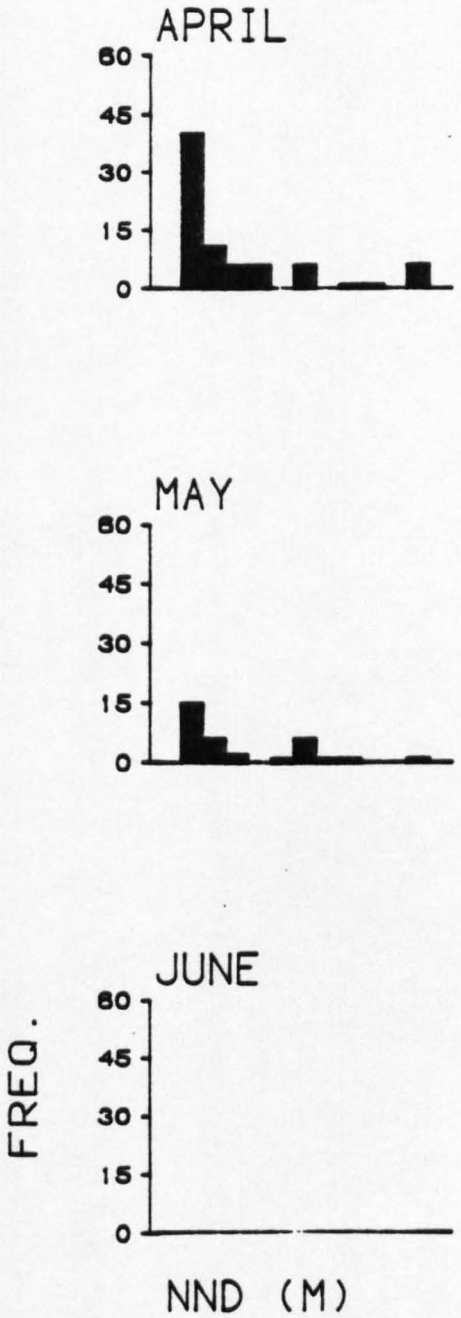


Table 2.2 Showing distance between 5 successive crabs at Eilean Mhartan.

Crab number	Distance from previous crab	Sex
1	1.0 m	Juvenile
2	0.1	Juvenile
3	0.1	Juvenile
4	0.1	Juvenile
5	0.1	Juvenile

Table 2.3 Showing distance between 5 successive crabs at Eilean Mhartan.

Crab number	Distance from previous crab	Sex
1	0.5 m	Female
2	0.5	Male
3	0.5	Male
4	1.0	Male
5	0.75	Female

Figure 2.27 Nearest neighbour distance of adult crabs by sex at Eilean Mhartan.

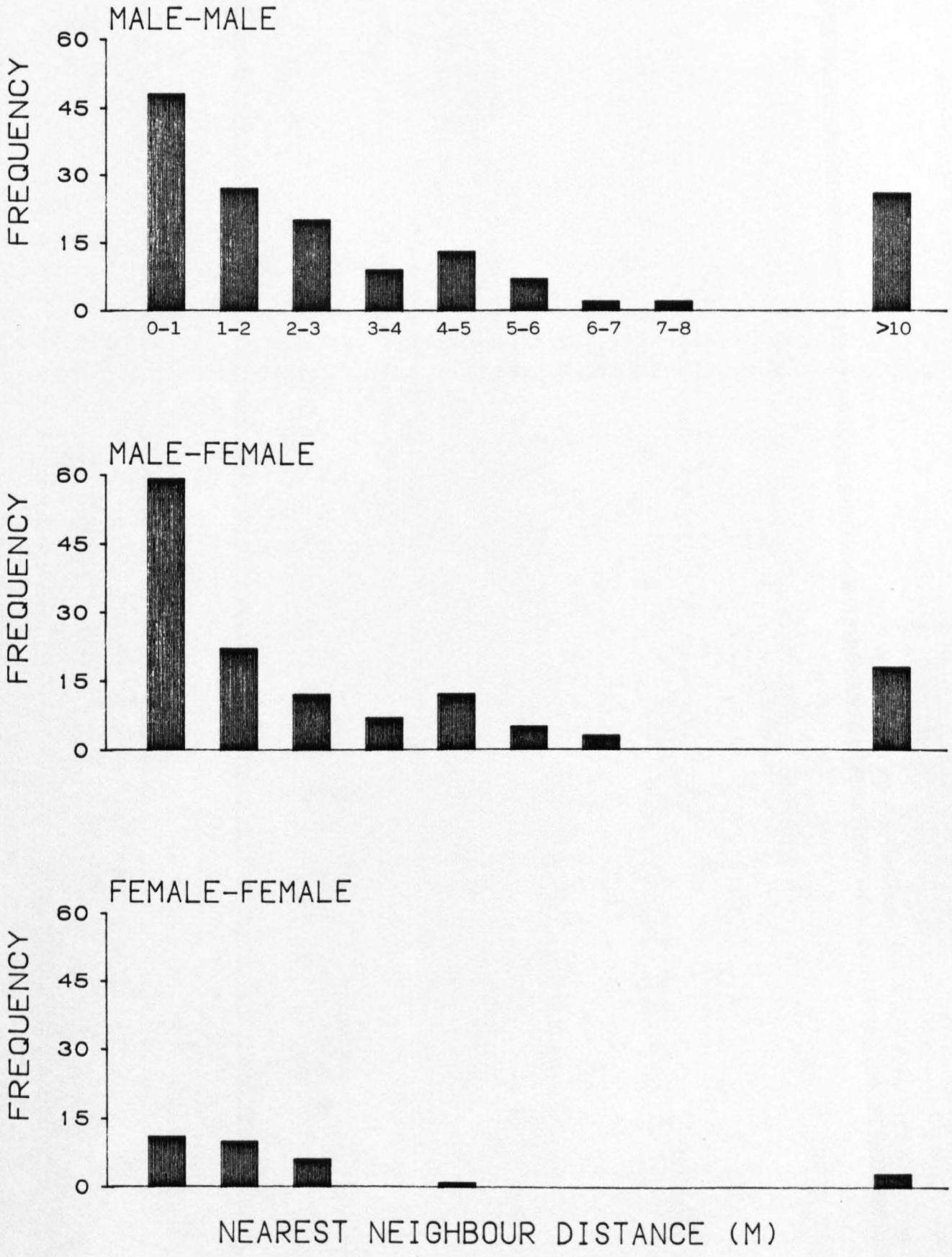
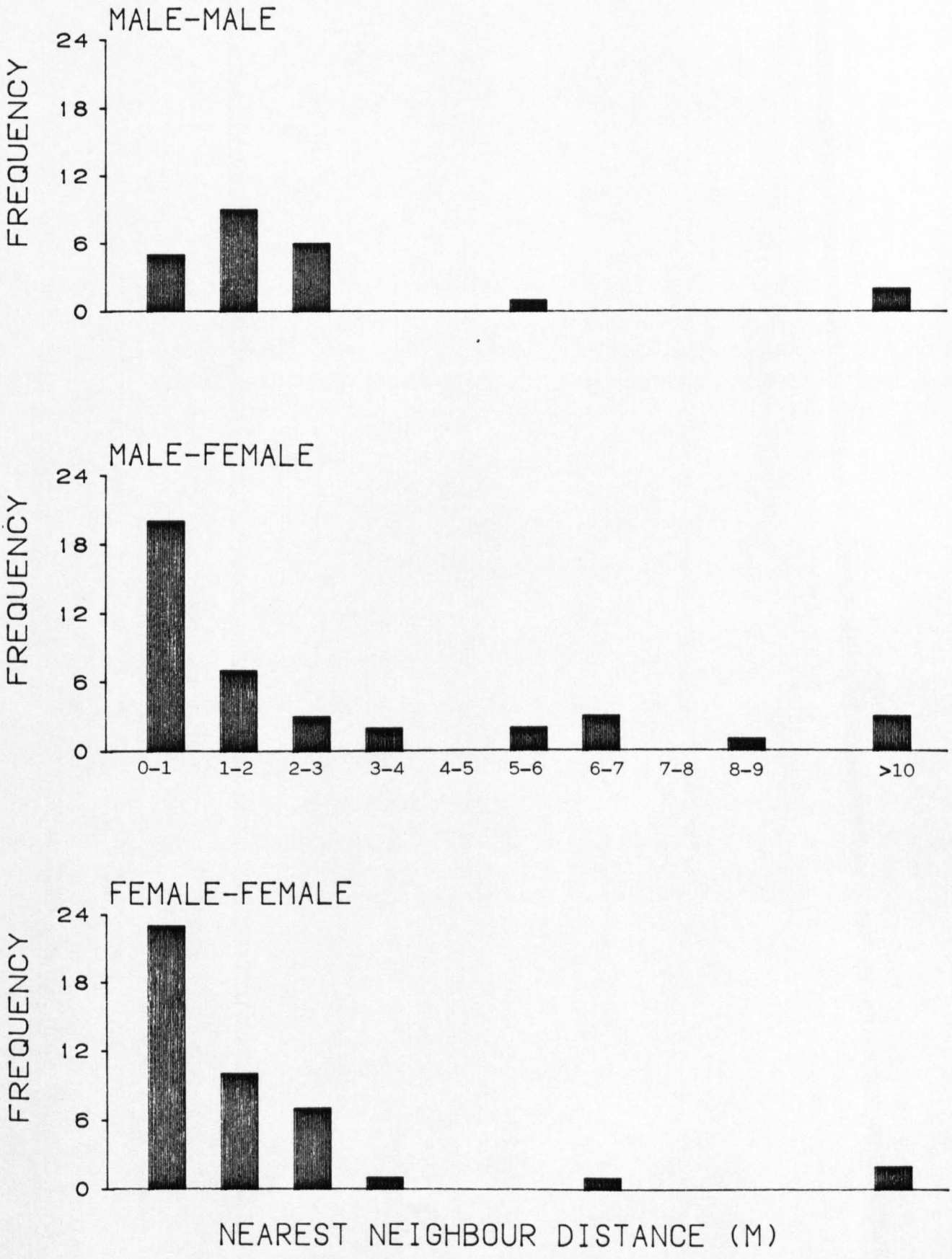


Figure 2.28 Nearest neighbour distance of adult crabs by sex at Port Lunna.



was felt to be too great to allow rigorous tests. However, the data indicate clearly that L. depurator is aggregated rather than randomly distributed at both sites and also that whatever causes this apparent aggregation, it is independent of the sex of the animals concerned.

Few studies have been attempted in which aggregation patterns of crustaceans have been quantitatively studied. Those which have been undertaken, generally involve small sediment dwelling animals where the numbers per unit volume can be readily quantified (Perry, 1980) or animals which live in burrows where the distribution of burrows can also be quantified easily (Nephrops, Chapman and Rice, 1971; Goneplax, Rice and Chapman, 1971; Atkinson, 1974). In each of these studies, quantification is possible due to the degree of site attachment by individuals, but with a highly mobile animal such as L. depurator, accurate measurement of individual spacing is almost impossible. However, even without strict quantification of the data it can be seen clearly that L. depurator is aggregated at the two sites studied. It is most likely that these aggregations are a response to localised food supplies and although no such locally abundant food supplies were immediately obvious, further investigation of both the food and feeding behaviour of L. depurator may elucidate the cause of the observed aggregations.

REPRODUCTION, GROWTH AND RECRUITMENT

L. depurator, in common with most other crustaceans, can only mate with a female which has just moulted. In order that a male is available at the moult and because of intermale competition, the

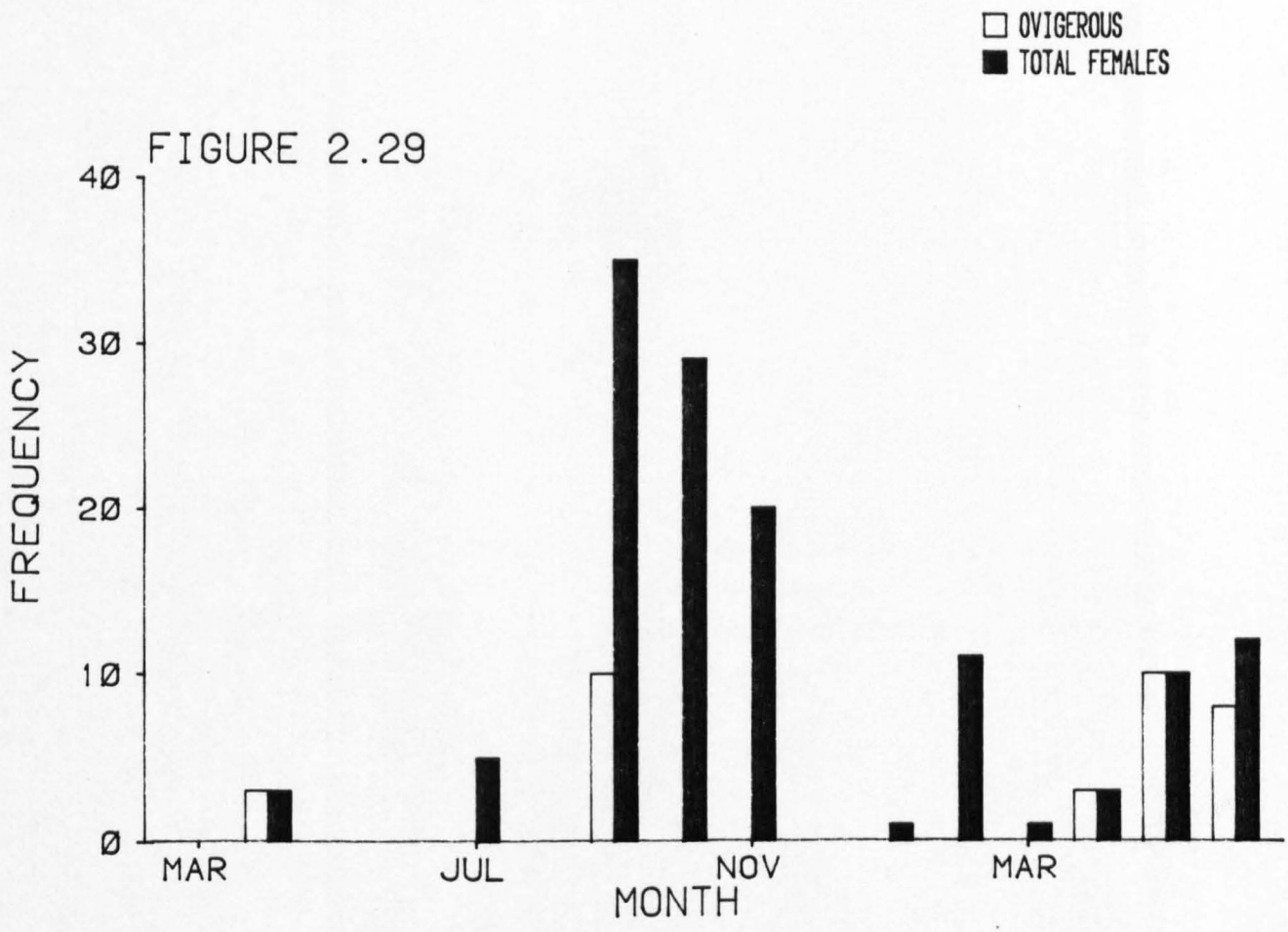
male is attracted to a female a few days before the moult and carries her beneath his sternum until moulting. During copulation the ventral surfaces of the crabs are opposed, the male generally embracing the female with his chelipeds and walking legs. Copulation may last for a long time, several hours in Carcinus (Warner, 1977) and subsequently the male carries the female beneath him until her exoskeleton is at least partially hardened. Taking into consideration the length of time that a male and a female must remain in contact for copulation to be completed, it is surprising that only four pairs of crabs were observed in making clasps during the course of this study. Three pairs were seen during the months of peak abundance, September-November, 1981 and one pair during June 1982.

Any crab involved in a mating couplet will inevitably be less capable of predator avoidance than any individual crab. It is also likely that other sexually mature male crabs should be attracted to the mating couplet by the pheromones released by the receptive female. This will almost certainly result in a higher than normal incidence of aggression. A combination of these factors may result in mating pairs seeking cover more persistently than single crabs and may account for the low incidence of mating pairs observed in the study area.

Female crabs which copulate just after moulting are in a depleted state and do not generally ovulate for some time (Warner, 1977). Sperm is stored in the spermathecae and remains viable for a long time. The eggs are fertilised during the act of laying as they must pass through the spermathecae on their way to the outside. The eggs

then adhere to the hairs on the pleopods and are retained and brooded in a mass under the abdomen of the female. In Cancer, ecdysis and copulation occur in autumn but egg laying does not take place until mid-winter of the following year, 14 months later (Pearson, 1908). The eggs hatch in July having been brooded for six months and a second batch may be laid the following year before the next ecdysis and copulation.

In the present study ovigerous females were observed in two distinct phases (Figure 2.29). At Eilean Mhartan they were first observed during April 1981 and again in September 1981. The following year, many more were observed during early summer (April-June). Data were also obtained during the restricted sampling period at Port Lunna and are shown on Figure 2.30. This observed double phase of brooding females agrees well with Allen (1967) who reported that female L. depurator produce two broods a year in the Clyde and Argyll sea area. Allen (1967) however states that ovigerous females are observed between January and June, and this is substantially different from the results of this study. At Loch Sween ovigerous females were observed only between April and September. An explanation for this difference is not immediately obvious but reports from different sea areas show a wide range of sightings. Ovigerous crabs have been recorded from the Plymouth area from March-October (Lebour, 1928), Bristol Channel from April-May (Crothers, 1966), Galway Bay from January-May (O'Ceidigh, 1962) and Ushant from March-August (Bourdon, 1965). The present study agrees most closely with Lebour (1928) for the Plymouth area and Bourdon (1965) for the Ushant sea area. Both of these sea areas are situated at the mouth of the English Channel and very far removed from the Clyde and Argyll sea area of which Loch Sween is a part.



Monthly distribution of ovigerous crabs at Eilean Mhartan.

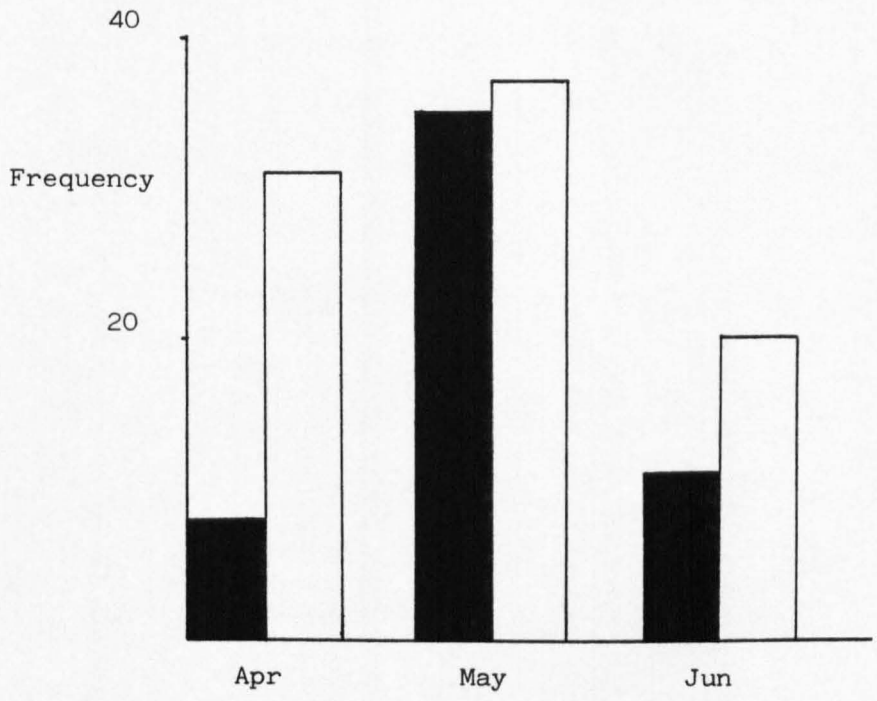


Figure 2.30 Monthly distribution of ovigerous crabs at Port Lunna.

For many crustaceans the time of spawning and hatching and the length of the incubation period vary with latitude and may be temperature dependent. For Nephrops, hatching begins earlier in the year off Portugal and in the Adriatic than in more northerly areas (Chapman, 1980). Although the reports mentioned above deal only with sea areas around the British Isles, there is little evidence to suggest a similar trend in L. depurator. However, for Nephrops the trend is quite clear and the large body of information which exists probably reflects the extensive sampling of the species due to its commercial importance. L. depurator has received much less attention than has Nephrops and it is therefore possible that the considerable variation in the sightings of ovigerous L. depurator may reflect lack of adequate sampling. It is also therefore possible that ovigerous crabs are present for more of the year than either the current study or previous studies have suggested.

Figures 2.29 and 2.30 show the number of ovigerous crabs observed in study areas and also include the total number of female crabs observed. In some months, particularly May and June, almost all the female crabs at each of the sites were ovigerous. Atkinson and Parsons (1973) noted that ovigerous Carcinus at Swansea, South Wales moved offshore to overwinter in the shallow sublittoral zone. At first sight the results of this study suggest a similar trend as no ovigerous crabs were observed during the winter months. However, transect surveys in winter in Loch Sween failed to reveal any swimming crabs in deeper water so there is little evidence to back this suggestion up. As discussed previously, further tracking of individuals using ultrasonic tags would almost certainly elucidate this.

Figure 2.20 shows the monthly abundance of juvenile swimming crabs (<20 mm carapace width) at Eilean Mhartan. Clearly, recruitment of small size class animals occurs principally between April and May. If Figure 2.20 is compared with Figure 2.19, it is immediately obvious that peak abundance occurs four months (September) after the corresponding juvenile peak (May). Growth in some Portunids can be very rapid indeed, particularly in warm water species such as Callinectes arcuatus with a growth rate of 8 mm per month (Paul, 1982) and C. sapidus, 10 mm per month (Tagatz, 1968b). Maturity in C. arcuatus takes between seven and nine months from the first juvenile stage (Paul, 1982) and there is no reason to assume that L. depurator should mature any more rapidly, particularly as it is a temperate water species. Therefore, the recruitment of juvenile crabs into the population at Eilean Mhartan in spring (April and May) can not be responsible for the observed increase in abundance of adult crabs in autumn (September and October). Further weight is given to this argument by examination of Figures 2.32 and 2.33 which show breadth-frequency histograms of male and female crabs. In neither case is there any evidence of a distinct group of small crabs which can be traced through consecutive monthly breadth-frequency distributions. This implies that the large number of large size class crabs (♂ , > 50 mm, ♀ > 40 mm) evident in autumn is due to movement of large size-class crabs into the area from elsewhere and not due to development within the area.

Monthly Distribution

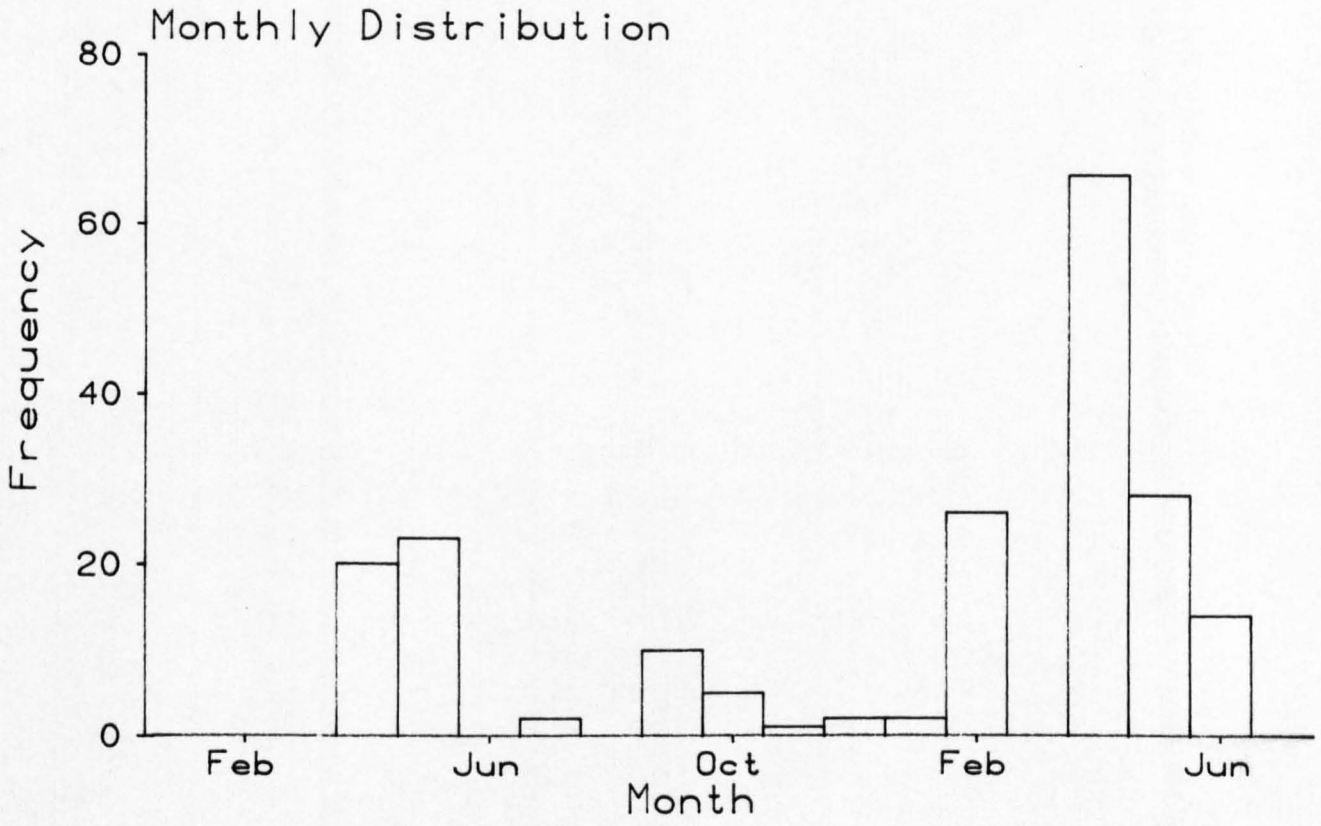


Figure 2.20 Monthly distribution of juvenile L. depurator (<20mm) at Eilean Mhartan.

Figure 2.32 Monthly size-class distribution of adult male L. depurator at Eilean Mhartan.

Size - class	Carapace width (mm)
1	< 20
2	20-25
3	26-30
4	31-35
5	36-40
6	41-45
7	46-50
8	51-55
9	56-60
10	61-65
11	66-70

Figure 2.32

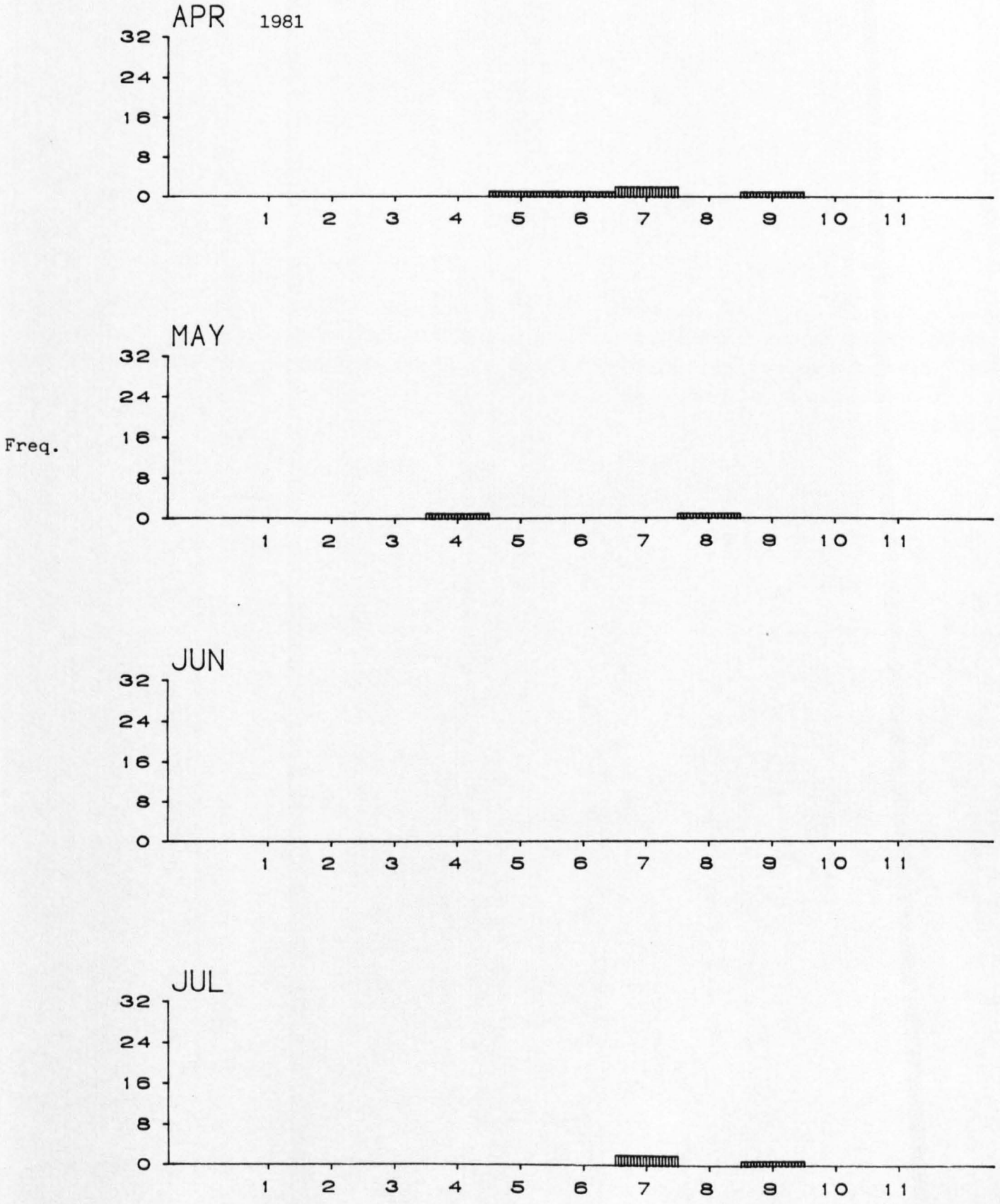

APR 1981
MAY
JUN
JUL
32
24
16
8
0
1 2 3 4 5 6 7 8 9 10 11
Freq.
Size - class

Figure 2.32

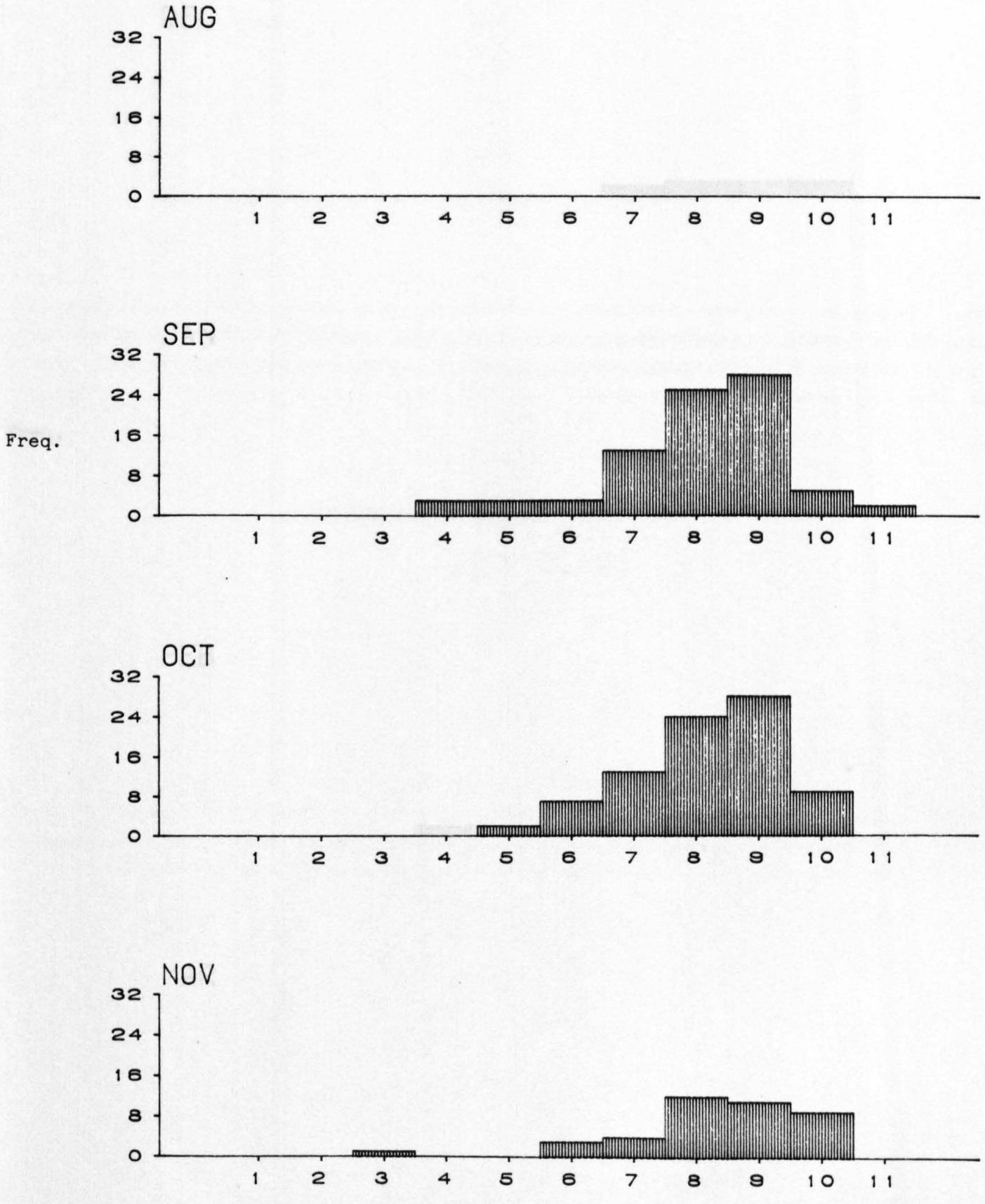


Figure 2.32

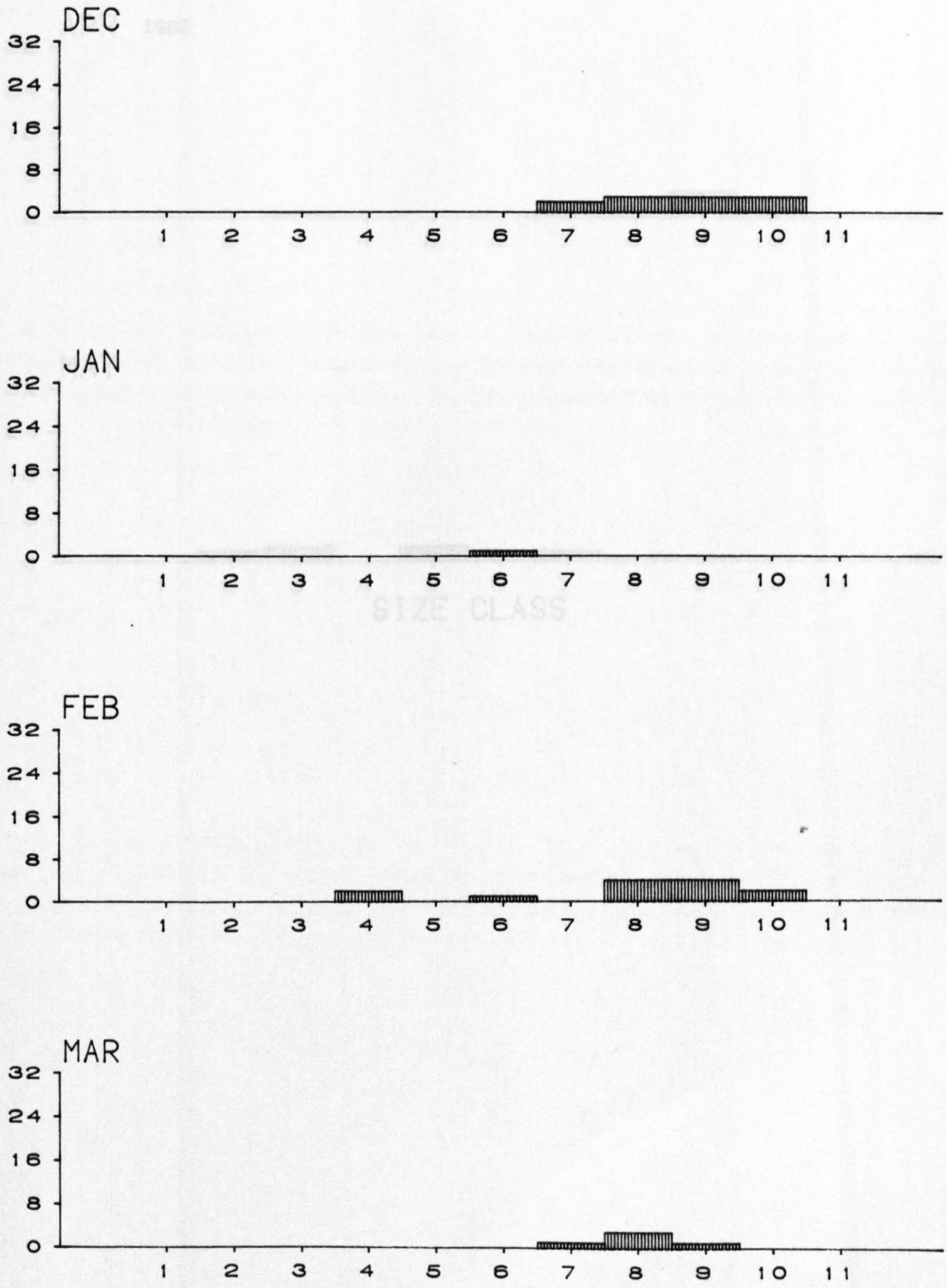


Figure 2.32

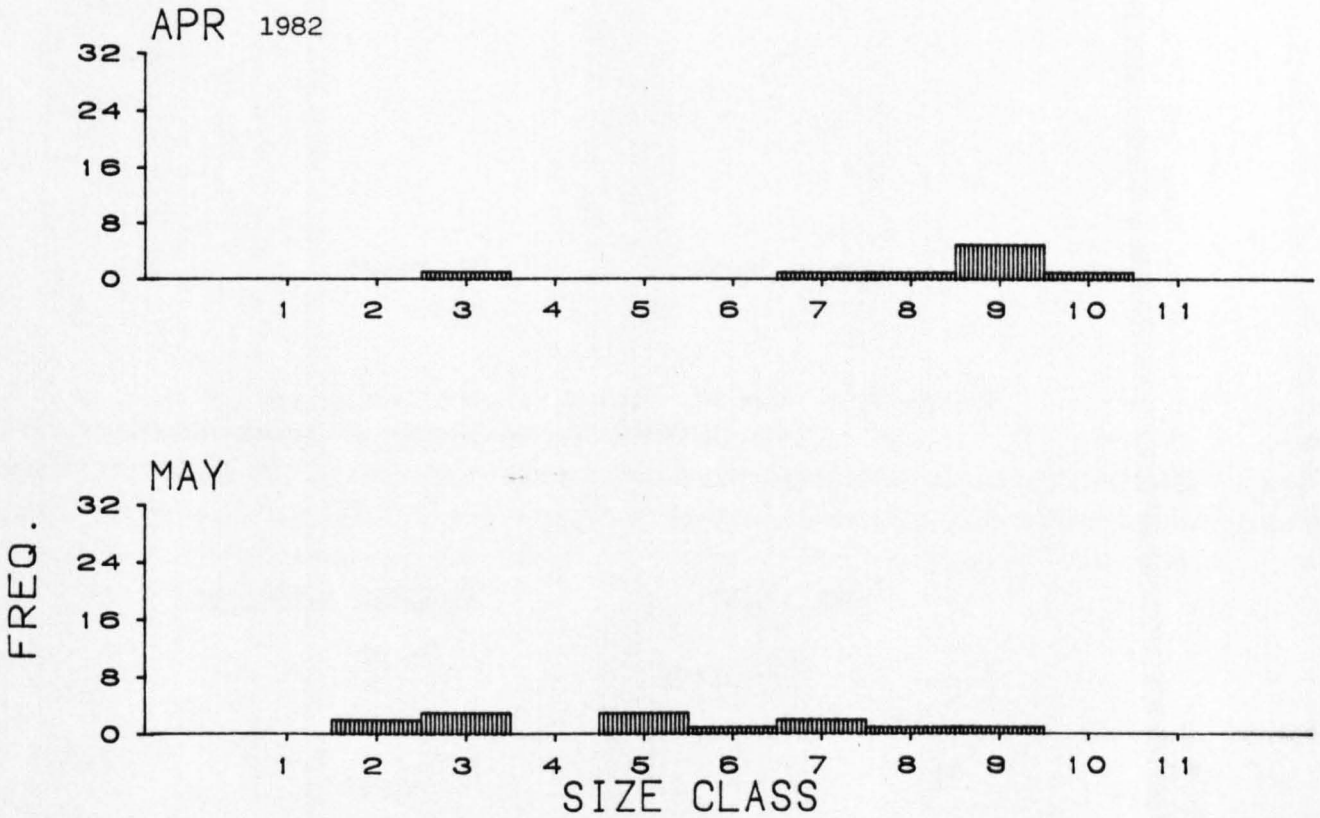

APR 1982
32
24
16
8
0
1 2 3 4 5 6 7 8 9 10 11
MAY
32
24
16
8
0
1 2 3 4 5 6 7 8 9 10 11
FREQ.
SIZE CLASS

Figure 2.33 Monthly size - class distribution of adult female L. depurator at Eilean Mhartan.

Size - class	Carapace width (mm)
1	< 20
2	20-25
3	26-30
4	31-35
5	36-40
6	41-45
7	46-50
8	51-55
9	56-60
10	61-65
11	66-70

Figure 2.33

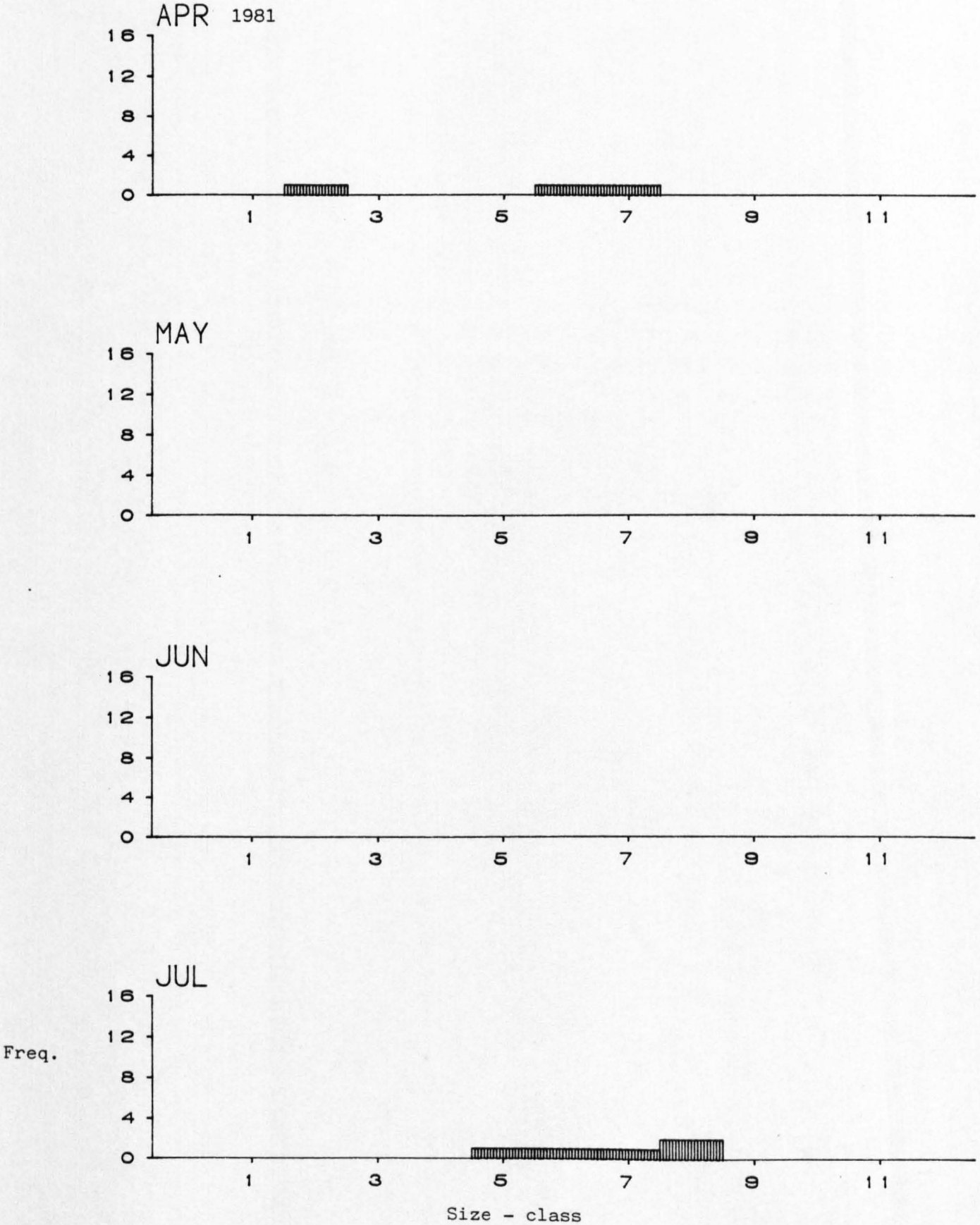


Figure 2.33

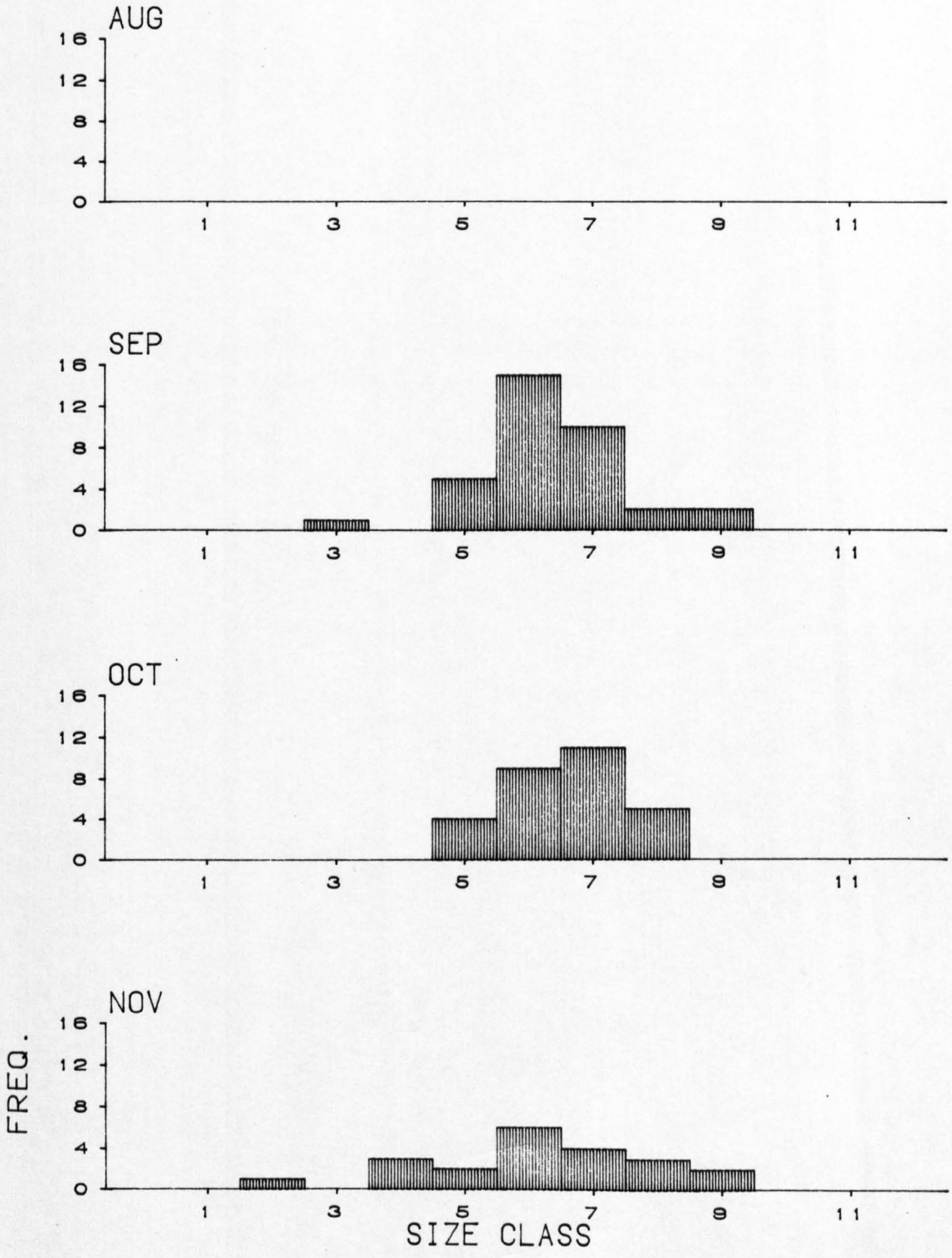


Figure 2.33

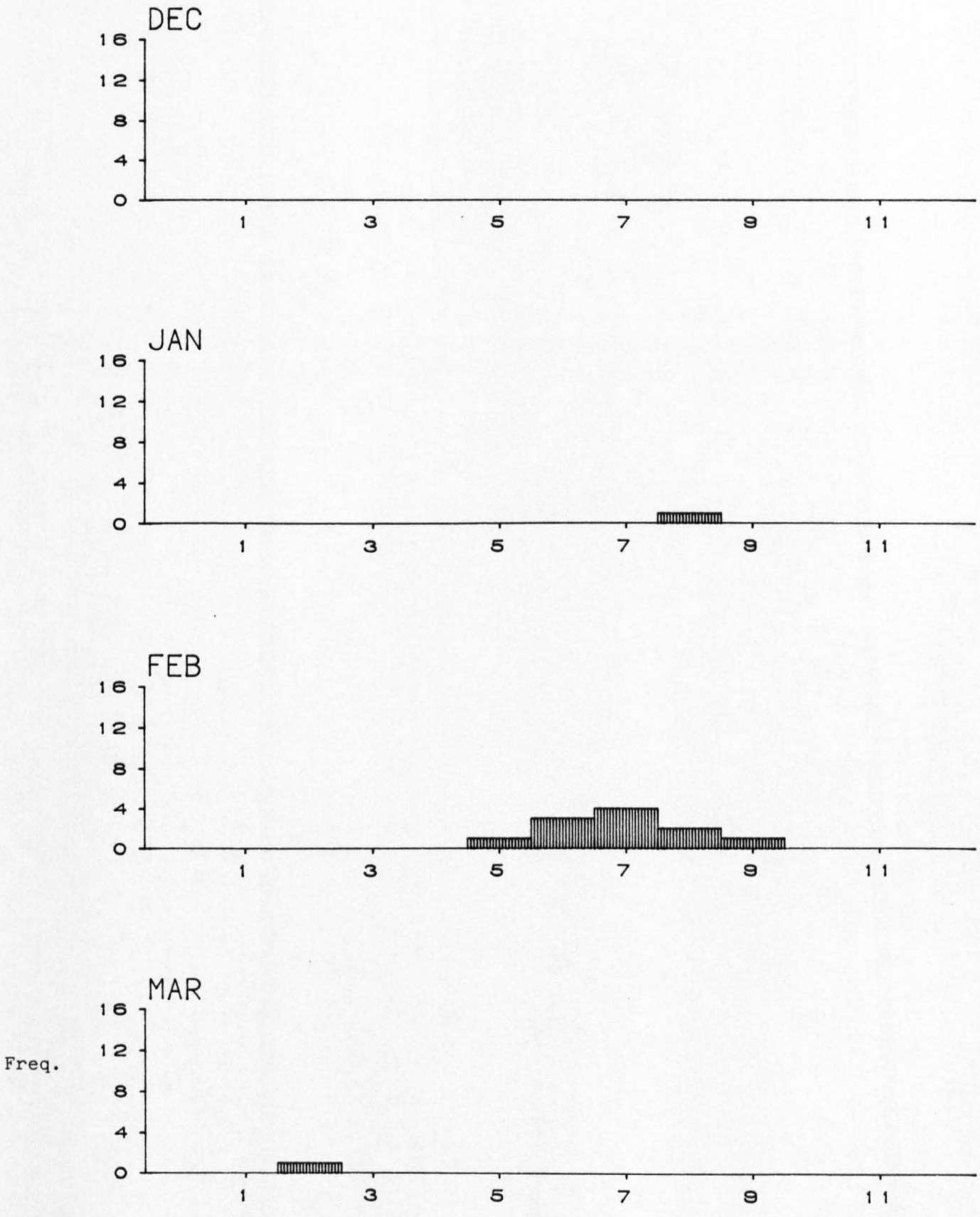
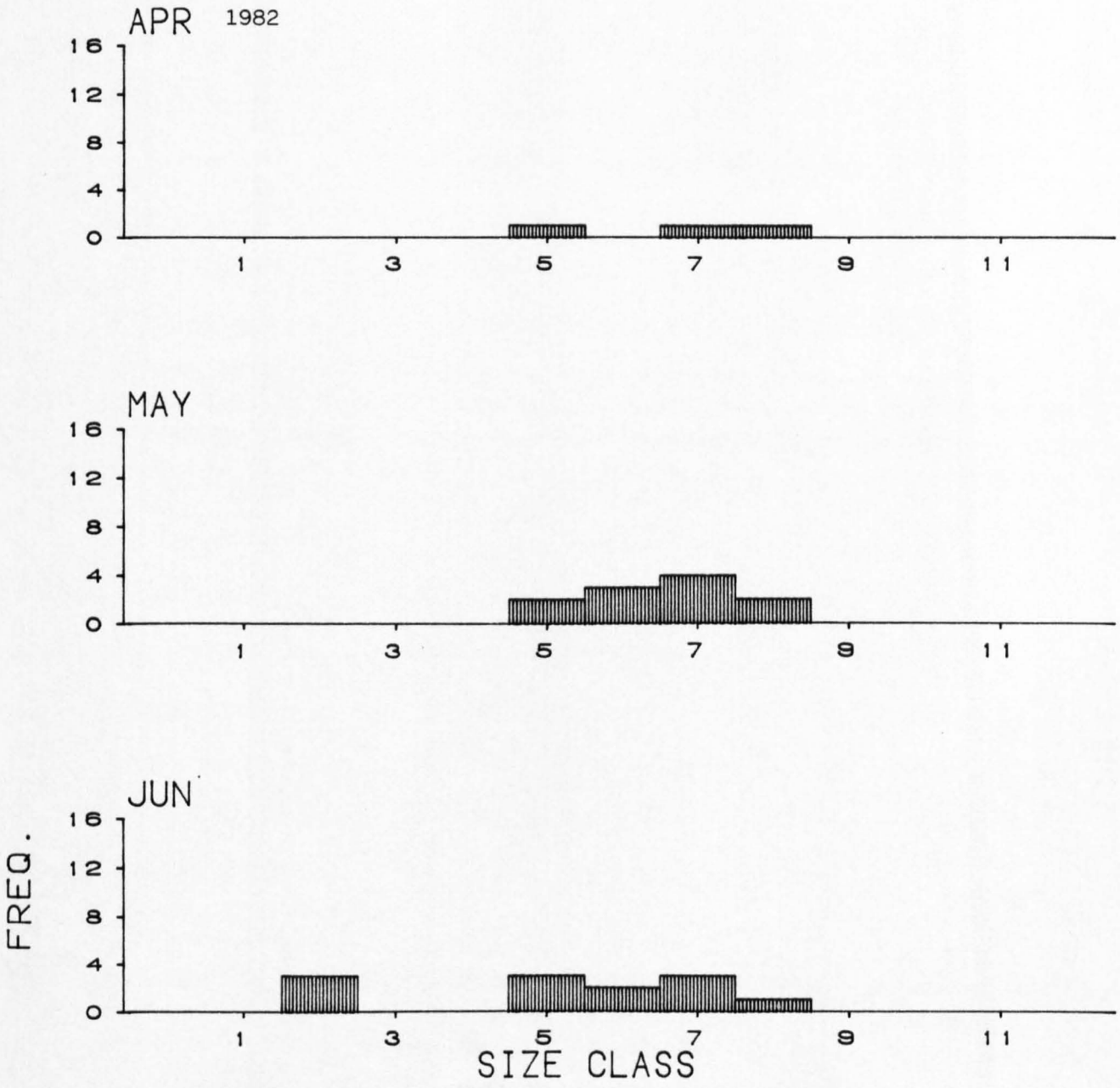


Figure 2.33



2-3.3 HABITAT UTILISATION

The relative use of habitat by crabs at the two sites is shown in Figures 2.34 and 2.35 while Figures 2.34b and 2.35b show a rough assessment of the relative availability of cover and substrate type. L. depurator at Port Lunna is found in three main types of position; hidden beneath weed, totally buried in the substrate, or standing on mud/silt substrate in exposed areas (Figure 2.35). These accounted for 89% of the animals observed, but of these three, crabs were most commonly found standing on the substrate without any cover. At Eilean Mhartan, a similar trend was evident and in addition, a large number of crabs (67; n = 553; 12%) were found standing on top of rocks and boulders (Figure 2.34). This reflects the nature of the study site at Eilean Mhartan where a large proportion (Figure 2.34b) of the site is composed of a shingle, rock slope (Plate 2.1). These positions accounted for 89% of the sightings but as with Port Lunna, crabs were most commonly found standing in exposed areas on a mud/silt substrate.

If crabs settled at random with respect to substrate or cover, then more crabs would be expected on or in silt/mud substrate than any other position at Eilean Mhartan, as this accounts for 65% of the habitat. Table 2.4 shows the observed and expected frequencies of Eilean Mhartan and Port Lunna for the three main types of position. At both sites there is a significant difference (Table 2.3) between the observed frequencies and expected frequencies. At Eilean Mhartan more crabs were found on or in the mud substrate than would be expected from the relative distribution of substrate types and similarly, fewer crabs than expected were found on the stone/boulder

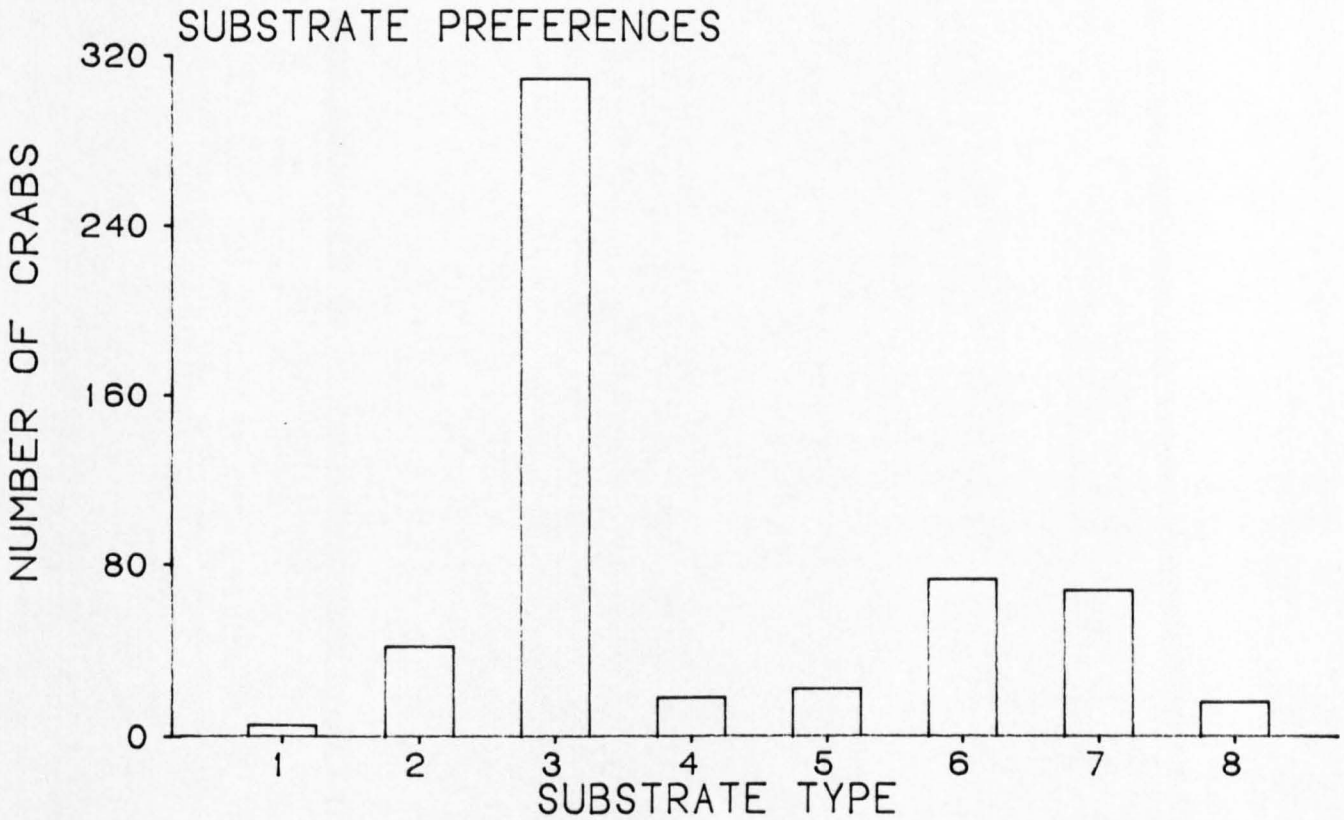


Figure 2.34 Substrate preferences shown by L. depurator at Eilean Mhartan.

Substrate Type	Description
1	On top of weed
2	Hidden underneath weed
3	Standing in open on mud/silt substrate
4	Sitting on substrate (in the open)
5	Semi-buried (in the open)
6	Totally buried
7	On top of stones or boulders
8	Under cover (other than seaweed)

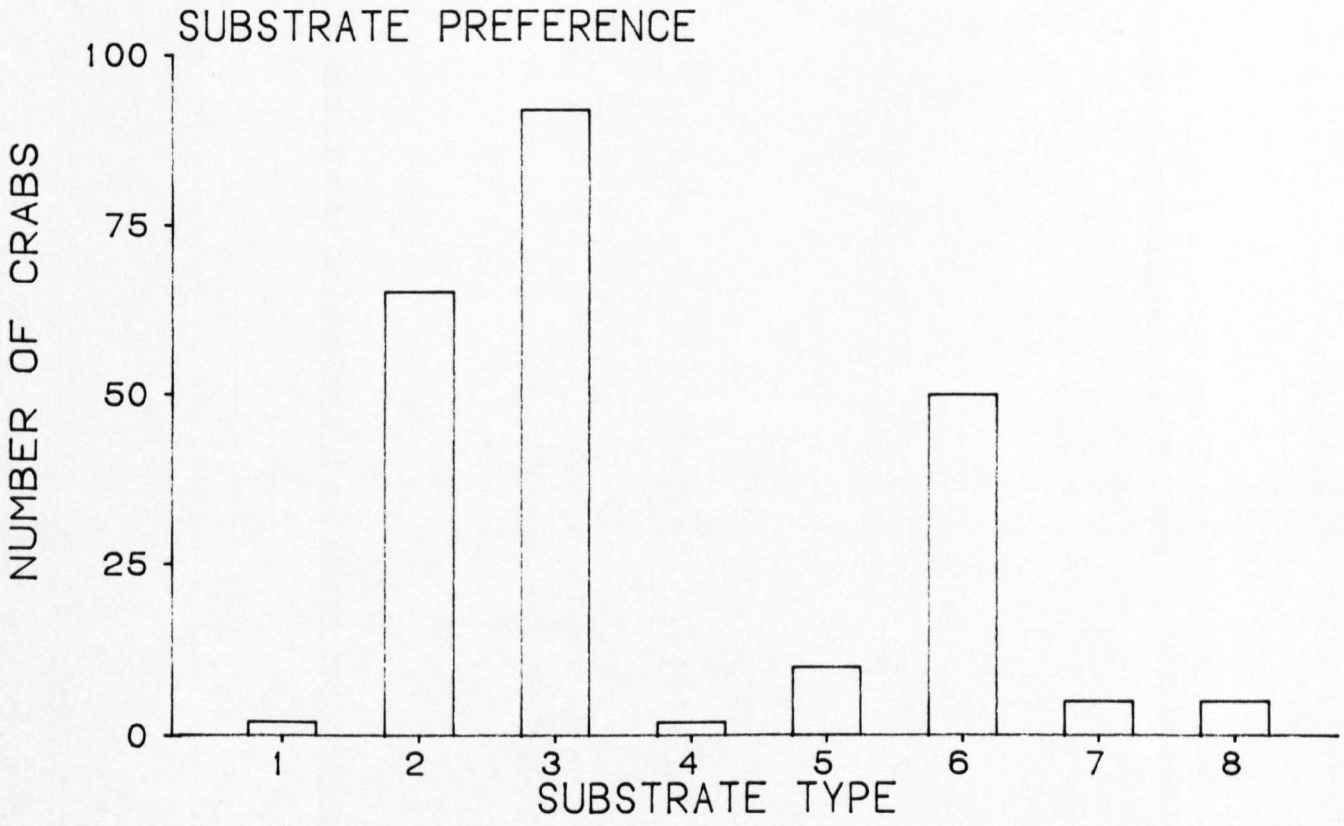


Figure 2.35 Substrate preferences shown by L. depurator at Port Lunna.
For description of substrate types see Fig. 2.34.

Figure 2.34b Percentage area of different substrate types at Eilean Mhartan.

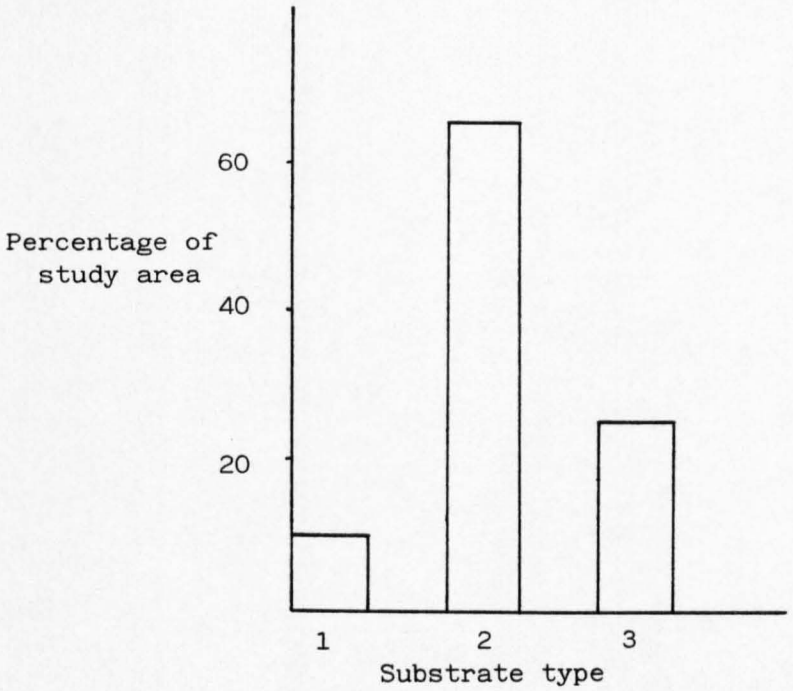
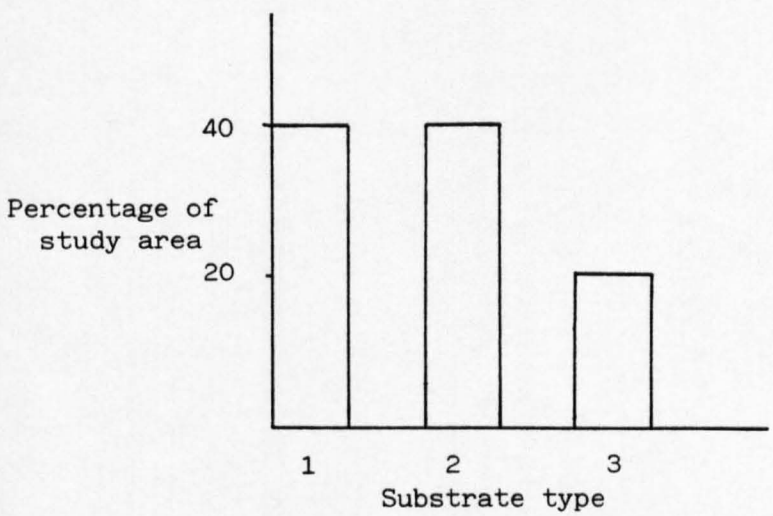


Figure 2.35b Percentage area of different substrate types at Port Lunna.



Substrate type	Description
1	Weed or other cover
2	Exposed mud/silt
3	Stones or boulders

Table 2.4

Eilean Mhartan (n=553)

Category	Observed	Expected
On or in mud	422	359
On or under weed	63	55
On stones	68	138

$X^2 = 47.7$ $p<0.001$

Port Lunna (n=232)

Category	Observed	Expected
On or in mud	154	93
On or under weed	73	93
On stones	5	46

$X^2 = 80.8$ $p<0.001$

Observed and expected frequencies for the three main types of position crabs were observed in at Eilean Mhartan and Port Lunna.

substrate. Similarly, at Port Lunna, more crabs than might be expected were found on or in mud/silt at the expense of on or under weed or boulder/stone substrate.

Figure 2.34 however contains data obtained over a 17 month period. It is possible that seasonal changes in habitat utilisation occur and are obscured in the overall data. Figure 2.36 shows the habitat utilisation at Eilean Mhartan broken down into monthly periods. Clearly no seasonal trend exists and habitat utilisation at the study sites remains constant throughout the year.

Of the crabs found on or in the mud/silt substrate, the majority of crabs were found standing on top of the substrate (Eilean Mhartan 309; n = 422; 73%: Port Lunna, 92; n = 154; 60%) as opposed to buried or semi-buried. This result at first appears surprising as one would expect that the more exposed a crab became, the greater the risk of predation would be. Conversely, the risk of predation decreases with increasing concealment. Swimming crabs may conceal themselves either by hiding under available cover such as kelp or by burrowing into the substrate. Animals falling into these categories accounted for 53% (124; n = 232) of the animals observed at Port Lunna and 24% (131; n = 553) of those at Eilean Mhartan. The higher values at Port Lunna almost certainly reflect the nature of the environment as Port Lunna has considerably more kelp than Eilean Mhartan.

However, L. depurator is an active animal which not only sifts through the sediment in search of small burrowing invertebrate prey but may also actively hunt larger more active prey (see 2-3.6).

Figure 2.36 Substrate preferences shown by *L. depurator* at Eilean Mhartan, on a monthly basis.

Habitat type	Description
1	On top of weed
2	Hidden underneath weed
3	Standing in open on mud/silt substrate
4	Sitting on substrate (in the open)
5	Semi-buried (in the open)
6	Totally buried
7	On top of stones or boulders
8	Under cover (other than seaweed)

FIGURE 2.36

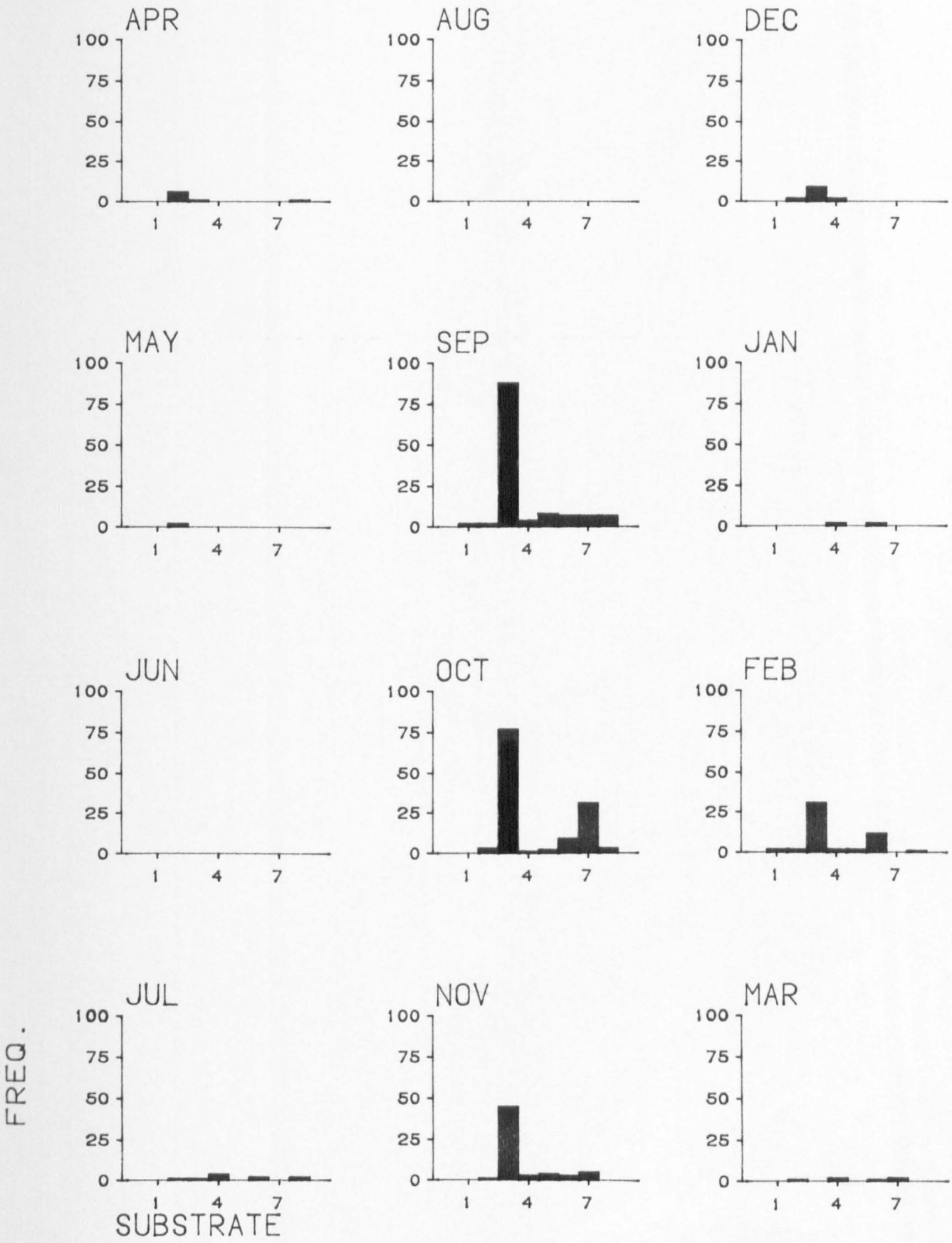
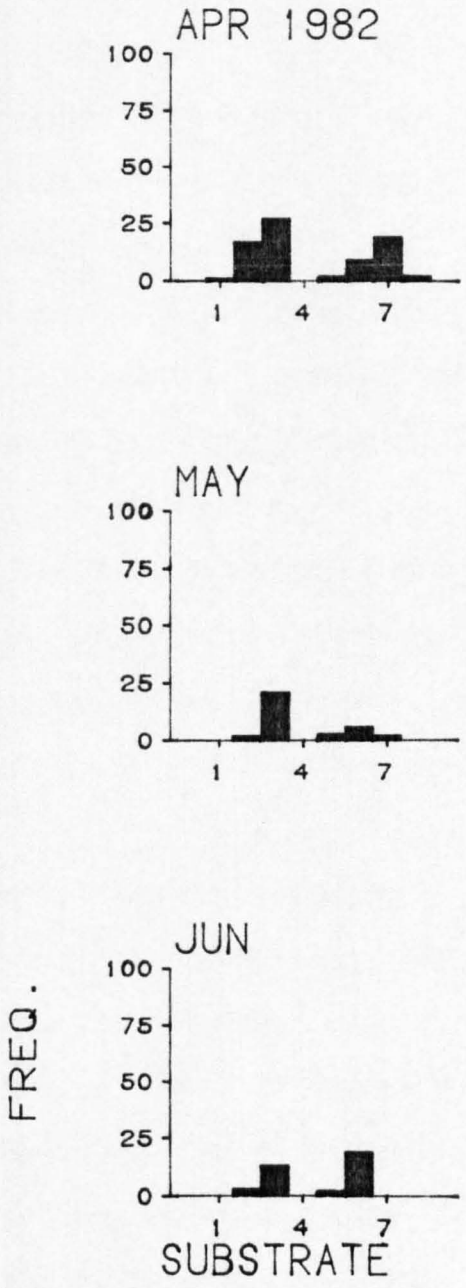

APR
AUG
DEC
MAY
SEP
JAN
JUN
OCT
FEB
JUL
NOV
MAR
100
75
50
25
0
1
4
7
FREQ.
SUBSTRATE

FIGURE 2.36 CONTD.



Concealment will therefore affect an animals foraging ability. As foraging is mainly carried out in more exposed areas, the benefits must be placed against the cost of predation. L. depurator is an extremely active fast moving crab capable of rapid movement to cover when disturbed. This response is most effective if the crab is standing on the substrate, as it can instantly use propulsion provided by the swimming legs. The response is much less effective if the crab is collapsed or sitting on the sediment. Under these circumstances the body must first be raised from the sediment before retreat is possible. Therefore, while moving across the sediment, the risk of predation may be reduced by remaining upright as opposed to sitting on the substrate. Examination of Figures 2.34 and 2.35 indicate quite clearly that the majority of crabs in exposed areas were observed standing on the sediment. At Eilean Mhartan, 422 crabs were observed in exposed areas; 90% (382) of these were raised on the sediment with only 10% (40) collapsed or semi-buried. At Port Lunna 89% (105) of crabs in exposed areas were raised above the substrate.

These patterns of habitat utilisation by L. depurator therefore seem to be associated with feeding and anti-predator behaviour. Crabs at both sites were shown to utilise exposed areas more frequently than might be expected in terms of availability of substrate type. This tendency towards utilisation of exposed mud/silt areas may be caused simply by animals moving from one area of cover to another; however, when encountered, most of these animals did not appear to be moving directly to cover, but appeared to be slowly probing the sediment with one or both chelipeds. This observation lends weight to the argument that much of the foraging of L. depurator is carried out on the mud.

Very few crabs were observed partially buried or sitting on the mud with most animals either standing upright or totally buried. It is postulated that total burial in the mud is an effective form of concealment for crabs which are not foraging or which have not found other cover and that animals which are foraging remain extended above the substrate in order that reaction to predators may be carried out quickly.

2-3.4 FOOD AND FEEDING BEHAVIOUR

Loch Sween provides a varied habitat with a rich invertebrate fauna. All groups of invertebrates are represented and there is little to suggest that food is in short supply. Potentially, therefore, a great many types of food are available to L. depurator. Almost without exception, each of the 422 crabs in exposed areas at Eilean Mhartan, and each of the 118 at Port Lunna, was observed probing the sediment with one or both chelipeds, while occasionally moving a limb to the mouthparts. This was presumably an attempt to locate small items of prey. No crab successfully located an obvious food item using this technique while under observation. However, 49 crabs were observed feeding on large prey items (Table 2.5) and these prey items were similar at both sites. The items listed represent a small proportion of items available in Loch Sween and while not providing a complete list of the food items of L. depurator, they give an insight into the feeding behaviour of the animal.

The most commonly observed food item in the diet of L. depurator was the sea squirt Ascidella aspersa. These are abundant at Loch

Table 2.5 Showing food items taken by *L. depurator* in the field.

Class	Species	Number of crabs observed eating food item	
Ascidiacea	*Ascidiella aspersa*	3	
Crustacea	*Carcinus maenas*	2	
	Pagurus bernhardus	1	
Asteroidea	*Asterias rubens*	2	
Scyphozoa	*Aurelia aurita*	5	Port Lunna
Hydrozoa	Not identified to species	2	
Cephalopoda	*Sepiola atlantica*	1	
Ascidiacea	*Ascidiella aspersa*	11	
Crustacea	*Carcinus maenas*	2	
Asteroidea	*Asterias rubens*	2	
	Marthasterias glacialis	1	
Scyphozoa	*Aurelia aurita*	6	
Gastropoda	Not identified to species	3	Eilean Mhartan
	Buccinum undatum	1	
Polychaeta	Not identified to species	4	
Osteichthyes (teleostei)	Gobies, not identified to species	3	

Sween. Fourteen crabs were observed holding A. aspersa, and in each case small pieces were transferred to the mouthparts by the chelipeds. These pieces of sea-squirt were ingested and not turned around by the mouthparts prior to rejection as comonly occurs when small stones are scraped of their faunal covering. L. depurator therefore appeared to be consuming the sea-squirts, not scraping small organisms from the surface. Eleven crabs were observed eating Aurelia aurita, the common jellyfish. These observations coincided with a bloom of Aurelia in the plankton during which underwater visibility was severely reduced due to the immense numbers of jellyfish present. Capture was a simple task for the crabs, accomplished by reaching up into the water column and grasping the jellyfish as they passed.

Representatives of many of the other invertebrate phyla were taken by L. depurator but in most cases capture of the prey was not observed. This, therefore, provided little information as to whether food was obtained by active pursuit and capture, or by scavenging. However, in some cases the method of capture was observed and in other cases, obvious. Cases where food was almost certainly obtained by scavenging, are illustrated by all four observations in which Carcinus was the prey item. Although considerably less mobile that L. depurator, Carcinus is much more heavily armoured and L. depurator would find it extremely difficult to kill an equal sized, healthy Carcinus. In each case in this study, the feeding crab was considerably smaller than the corpse on which it was feeding, suggesting the food item was obtained by scavenging.

One swimming crab was caught while in possession of Sepiola atlantica, the little cuttlefish. The mode of capture was not observed, but on release by the swimming crab, the cuttlefish escaped rapidly. This indicated that the cuttlefish was healthy and active and that capture was probably by active means. In addition, on two separate occasions, active capture of small fish, Gobius species, was observed. In both cases, the crab remained totally inactive on the substrate until the fish moved within lunging distance. The swimming legs were used for propulsion and both chelipeds were used to grasp the fish. On a third occasion a goby was identified as a food item, but as the fish was badly mutilated, it was not possible to deduce whether this fish had been actively captured or not. Many other observations fall into this category.

A number of interesting points are raised by this food and feeding behaviour data. Over 62% of all crabs (n = 795) were carrying out sediment sifting motions when first observed by the divers. On no occasion was any obvious food item transferred to the mouthparts, but this may in part reflect an inability on the part of the divers to identify small items at a distance. Undoubtedly, L. depurator obtains some of its diet in this way, but this may be of lesser importance to the crab than the other large prey items discussed in this section.

L. depurator appears to be an opportunist feeder, with items such as A. aurita being taken during periods of high availability. Similarly, on two occasions when gobies were taken, no attempt was made to stalk or to lure the prey. The items appeared to be taken simply as the fish moved within striking distance of the stationary crab. Presumably the cuttlefish (S. atlantica) was taken in the same way.

Paul (1981) in a study on the diet, feeding and predatory activity of two species of Pacific swimming crabs, stated that although fish were abundant in the study area, and commonly eaten by the crabs, it was doubtful that Callinectes arcuatus could kill large and healthy fish. Hay (1905) and Truitt (1939) reported that C. sapidus frequently stalked fish and Kwei (1974) noted that C. latimanus can stalk and kill Tilapia species. Further laboratory studies by Paul (1981) indicated that, whilst C. arcuatus is capable of killing small or weak fish, it is most probable that much of the fish eaten by the crabs is through scavenging dead fish.

In the present study L. depurator was not observed stalking fish prey and on both occasions when capture of fish was observed, there was nothing to suggest that the prey items were in any way unfit or unhealthy. It appears therefore that L. depurator is capable of active capture of small healthy fish prey and that at least same of the fish eaten by the crabs is obtained in this way. On one occasion a number of swimming crabs were being chased by divers. This resulted in one crab swimming directly over a conspecific semi-buried in the mud. The semi-buried crab darted up and grabbed the passing crab. On sinking to the substrate again, the captured crab was released and both crabs moved off in separate directions. It is possible that this type of capture is a reflex response to passing objects and in this instance the object was released upon the realisation that it was a conspecific. Further laboratory work may establish the nature of this response.

Laboratory studies indicated that if maintained at high densities, and deprived of food, L. depurator will resort to attacking and eating

conspecifics. This finding is not surprising as many other crustaceans held under similar conditions will resort to cannibalism. However, the conditions necessary for this rarely occur in the natural environment and presumably conspecifics do not form much of the diet of L. depurator.

Crabs were also obvserved cracking open the shells of small Mytelis edulis (common mussel) and removing small hermit crabs (Pagurus bernhardus) by cracking open their gastropod shells in the laboratory. These items are common at both study sites and may form an important part of the diet. In the laboratory, however, feeding on these items occurred only when specimens were small, and it seems unlikely, due to the lightly armoured nature of the chelipeds in L. depurator that predation on Mytelis and Pagurus occurs on any but the smallest of specimens in the field.

The results reported in this section reflect only those items taken while under observation by the author. Undoubtedly other species not mentioned here will form part of the diet of L. depurator. However, the results show L. depurator to be essentially a predator of sessile or slow moving benthic macroinvertebrates and small vertebrates. A similar slow moving benthic macroinvertebrate diet has been widely reported for many larger portunid crabs including C. sapidus off the east coast of the United States (Darnell, 1958; Tagatz, 1968; Jaworski, 1972), C. latimanus in West African coastal lagoons (Kwei, 1974), Scylla serrata in South African and Australian waters (Hill, 1976) Carcinus maenas on European and North American shores (Munz et al, 1965; Crothers, 1968; Ropes, 1969) and Portunus pelagicus in Australian waters (Williams, 1982).

While the diet of L. depurator has been shown to be similar to that reported for a number of other species, in at least one species, Portunus pelagicus (Williams, 1982), the flexibility with regard to its diet has been shown by marked differences between diets of nekto-benthic and intertidal crabs. Local availability of food is obviously one of the major factors affecting a crabs diet and this diet of L. depurator may therefore be expected to vary from locality to locality.

2-3.5 ANTI-PREDATOR RESPONSES

The main natural predators of L. depurator are cephalopods and ground feeding fish such as poor cod (Trisopterus minutus), dogfish, plaice and skate. While their main diet is fish, seals are also known to feed on benthic crustaceans and as such may be a source of predation on L. depurator. Both the spotted dogfish (Scyliorhinus canicula) and the seal (Phoca vitulina) are common in Loch Sween (personal observation) and may account for most of the predation on healthy swimming crabs. Few flatfish or other ground feeding fish were observed at the study sites although the noise generated by the divers may have frightened any such animal locally, leading to an inaccurate estimate of numbers. These fish may therefore still represent a source of predation on L. depurator in Loch Sween. Damaged or diseased swimming crabs may also fall prey to other crustaceans, including conspecifics, although the incidence of this is likely to be low compared to that of the larger predators such as dogfish.

No natural predator/prey interactions were observed in the field, but L. depurator was seen to display three distinct types of escape response from an approaching diver. Although different in many respects, the stimulus presented by an approaching diver must be relatively similar to that of any large predator such as a seal. The escape responses shown to the divers may therefore represent the natural escape responses of L. depurator to a large predator. The three types of response shown were;

1. Instant burial response.
2. Zig-zag response.
3. Cover response.

1. Instant burial response. This type of response was shown only by juvenile crabs (< 20 mm) and involved an immediate flattening of the body against the substrate while pushing the body backwards and downwards through the sediment. Simultaneously, the swimming legs were used to cover the carapace with sediment scooped up from behind the body. Complete burial by this method could be achieved within approximately three seconds.
2. Zig-zag response. This type of response was shown mainly by large crabs found on exposed areas of sediment and involved rapid zig-zag swimming movements across the top of the sediment. The swimming legs were used as a means of propulsion, and in the process sediment was disturbed into suspension thereby reducing visibility. Large crabs were capable of producing large clouds of silt in a short time and this may greatly increase the ability of the crab to avoid detection. Some small adults (>30 mm) and juveniles (< 20 mm) also showed this

response but were generally less effective at producing a silt 'screen' than larger crabs.

3. Cover response. This was shown by adults and juveniles alike and involved immediate, high speed swimming towards the nearest point of cover. Type of cover did not appear to be important and man-made articles such as oyster trays were chosen as readily as fronds of seaweed. On reaching cover, crabs did not always remain stationary, but often continued to move while hidden beneath the cover, thereby making detection more difficult. Frequently, if the substrate allowed, crabs also buried themselves while hidden beneath cover.

These different responses did not appear to depend on the distances from the diver when the reaction took place but did seem to reflect the nature of the environment. If crabs were situated close to available cover, the response was almost invariably the cover response and was shown by animals of all sizes. This type of fleeing response is one of the commonest behavioural responses of prey animals to predatory attack (Humphries and Driver, 1971). If, however, a predator is swifter than the prey, this fleeing response is not so effective. The prey's chances of escape then depend largely on zig-zag or protean behaviour, particularly if no hiding place is available (Humphries and Driver, 1971). The theoretical possibility that irregular behaviour might serve as a device against predators was suggested by Chance and Russel (1959) and the existence of these protean displays was confirmed by Humphries and Driver (1967) who defined protean behaviour as that behaviour which is sufficiently unsystematic to prevent a reactor predicting in detail the position or actions of the actor. Protean fleeing has been described for many

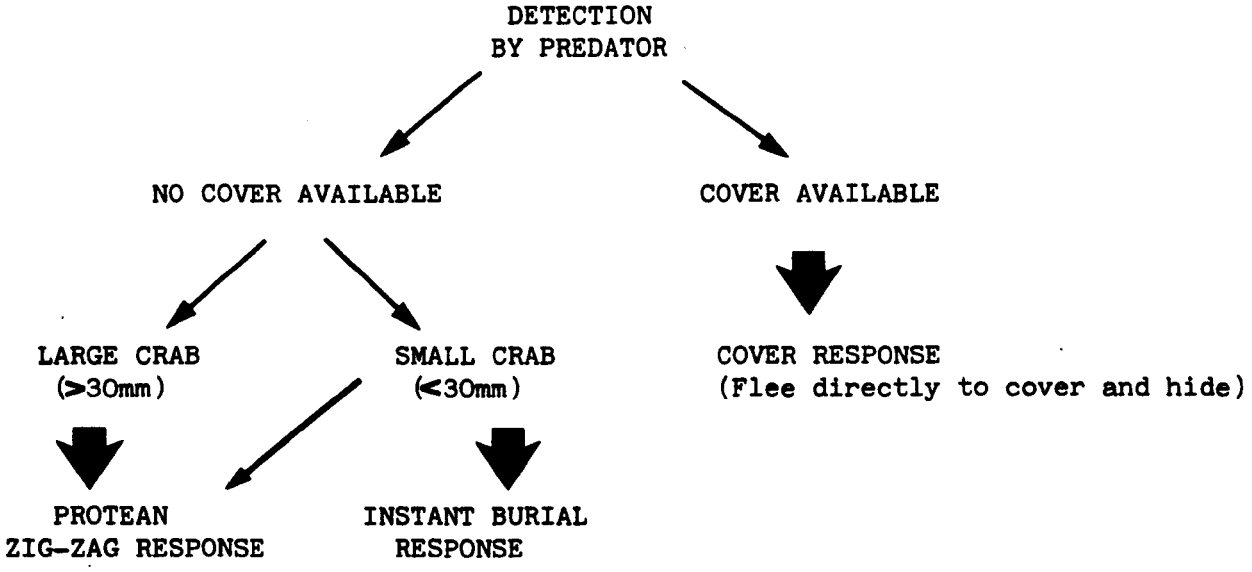
species and include the European hare Lopus europaeus, the nandu, Rhea americana, ptarmigan Lagopus lagopus (Tinbergen, 1951) and the copepod Calanus (Marshall and Orr, 1955).

In the present study large L. depurator displayed protean fleeing responses to approaching divers and this response was increased in effectiveness by disturbance of the sediment by the swimming legs. Small swimming crabs ($<$ 30 mm) rarely showed this protean behaviour and tended to adopt the instant burial response when disturbed in areas with no cover available. One possible reason for this observed difference in behavioural responses is that small crabs may not be able to move rapidly enough to ensure the effectiveness of the protean response. Under these circumstances, rapid burial into the substrate may be the next most effective response as any attempt to move across the substrate would almost certainly lead to capture by a swiftly moving predator.

Figure 2.37 summarises the responses shown to a potential predator by crabs at Loch Sween.

Humphries and Driver (1971) suggest that protean displays operate by arousing conflict and interfering with the information processing capacities of the predator, lengthening reaction time and reducing the effectiveness of predatory mechanisms. They also suggest that in contrast to other forms of anti-predator response, protean displays are resistant to learned countermeasures by the predator, as learning depends on the recognition of repeatable relationships. To the extent to which the relationships involved in protean displays are not repeatable, the predator is prevented from learning how to deal with them (Humphries and Driver, 1971).

Figure 2.37 Summary of escape responses shown by L. depurator to approaching divers.



Clearly, this spectrum of anti-predator responses shown by crabs at Loch Sween may have distinct survival value allowing crabs to forage on exposed areas while also allowing chance of escape from predators. In addition, the field observations indicate that a certain amount of flexibility exists and that different responses may be adopted under different circumstances. Such flexibility may also have a distinct survival value.

2-3.6 PHYSICAL CONDITION

Autotomy is the voluntary shedding of a limb by snapping it off at the base. A preformed breakage plane occurs at the base of each limb but is secured in an intact crab by a cuticular plug which bridges the plane on the antero-dorsal side. To achieve autotomy this plug must be sheared away, a process accomplished by particular contractions in the levator muscles (McVean and Findlay, 1976). Crabs autotomise limbs which are badly damaged or siezed by an attacker (Warner, 1977) and loss of body fluids following autotomy is prevented by an internal partition which remains behind as a seal over the stump. This is soon supplemented by clotted blood which accumulates to form a scab. Loss of a limb by a crab can only occur due to this autotomy reflex or direct physical removal by another animal. The damage may be caused during successful escape from predatory attack, during intraspecific aggression or under certain circumstances as a result of trawling or other fishing methods. No such trawling or fishing was carried out in the study area, consequently crabs showing an incomplete limb complement were

designated as having been involved in some form of predatory attack or intraspecific aggression.

Missing limbs can only be replaced by moulting. Loss of limbs stimulates the onset of the next moult but may decrease the size increment since resources are diverted to the regenerating limbs. Regeneration starts soon after autotomy by the formation of a small limb bud (Adiyodi, 1972). The bud develops during intermoult into a tiny limb folded up inside a flexible sack which projects from the stump. During premoult the bud grows rapidly and when the crab moults its length is about a quarter of the carapace width. Immediately after the moult the regenerated limb unfolds and expands but is still somewhat smaller than the other limbs. It regains its full size after the next moult. In many crustaceans, including barnacles, crayfish and the lobster, Homarus, moulting and growth continue throughout life although moults become spaced further and further apart. In others, such as some crabs (Maja, Carcinus) moulting and growth cease with the attainment of sexual maturity or of a certain size or after a certain number of instars (Warner, 1977). This terminal anecdysis in crabs is not detectable except by histological examination although outward signs such as a damaged exoskeleton or an encrusting sessile epifauna may be reliably used as indicators of this condition (Warner, 1977). L. depurator almost certainly shows terminal anecdysis, although this has not been studied systematically. During this study any animal supporting an encrusting epifauna was considered as being an old crab during terminal anecdysis.

At Eilean Mhartan a total of 553 crabs were observed and the physical condition of each was noted. Of these 553 crabs, only 40 (7%) were seen to have one or more limbs missing while only 15 (3%) crabs were heavily encrusted. Two of these heavily encrusted crabs had a least one limb missing. However, heavily encrusted crabs were not more likely to have missing limbs than non-encrusted crabs (X^2 = 0.723; 1 d.f., N.S.). Heavily encrusted crabs or crabs in terminal anecdysis might be expected to be more lethargic and less agile than younger healthier adults. Under these circumstances they might also be expected to be more prone to attack by predators and consequently show a higher degree of limb damage. The results indicate however that this is not the case. An alternative explanation is that heavily encrusted crabs are unable to effectively avoid predation and as such are removed from the population altogether. This may in part account for the low number of animals of this type observed throughout the study.

Of the 40 crabs without a full limb complement, 25 were male, 8 were ovigerous females and 7 were non-ovigerous females (Table 2.6). In all cases crabs with missing limbs were larger than 30 mm carapace width. All juveniles observed had a full limb complement. Table 2.6 shows that in general female crabs are no more likely to have missing limbs than are male crabs. However, ovigerous females are more likely to have missing limbs than either non-ovigerous females or males (X^2 = 5.36, 1d.f., $p < 0.05$; X^2 = 3.9, 1 d.f., $p < 0.05$, respectively). Female crabs carry eggs on the pleopods of the abdomen for a period of time before the eggs are laid. Given that the presence of eggs is not detectable unless the animal is studied closely, and that there is no evidence to suggest that females are less

active than other crabs, it is unlikely that during this period of berry, a female crab should experience a higher level of predatory attack than any other crab. It is possible, however, that any such ovigerous crab may have an increased awareness which may help in the protection of the eggs and which may heighten the autotomy reflex. These conditions could result in the higher incidence of limb loss observed in ovigerous females at Loch Sween, but further laboratory work is needed to fully understand this problem.

Table 2.7 summarises the extent of limb loss shown by crabs at Loch Sween over the study period. It is immediately obvious that the most commonly lost limbs are the chelipeds. This finding is not surprising as the chelipeds will almost certainly be used as a means of defence against any attack. Consequently, these are the limbs which are most likely to be damaged or removed. Warner (1977) states that the mangrove crab Goniopsis sometimes responds to a human attacker by pinching hard with a chela and then autotomising the cheliped. The chela continues to pinch after autotomy, often allowing the crab to escape. This particular response was noted on two occasions at Eilean Mhartan when male crabs were being processed, and it seems likely that a similar response may be used to aid escape from other attackers.

One crab at Eilean Mhartan was damaged to the extent of having only two walking legs and both swimming legs intact. This type of damage was rarely observed however, and the majority of crabs overall (94%) had a complete complement of limbs.

Table 2.6 Showing distribution of missing limbs with sex at Eilean Mhartan.

Category	Number with missing limbs	Number with full limb complement
Male	25	245
Female (non-ovigerous)	7	89
Female (ovigerous)	8	26

$X^2=5.36$ $p<0.05$

$X^2=3.9$ $p<0.05$

n.s.

Table 2.7 Summary of extent of limb loss shown by crabs at Eilean Mhartan and Port Lunna.

Missing limbs	Eilean Mhartan Number of crabs	Port Lunna Number of crabs
One cheliped	18	5
Both chelipeds	9	3
Cheliped plus one or more ambulatory legs	7	0
One or more ambulatory legs	3	0
One swimming leg	3	0
	n= 40	n= 8

In laboratory populations where crabs are held at high density (>10 crabs/m^2) up to 50% of the crabs may be found to have missing limbs (personal observation). Hazlett (1975) also found that groups of hermit crabs maintained at relatively high densities were more aggressive than low density crabs and won encounters with low density crabs more frequently than expected by chance. In the current study the physical damage observed in the field is low compared with that known to exist in the laboratory, and suggests a low level of escalated physical aggression within the field populations. This is supported by the low number of intraspecific aggressive interactions observed in the field (2-3.7). The alternative suggestion that levels of predatory attack are also low does not necessarily hold as the low incidence of physical damage may simply reflect a low rate of successful escape from any such attack. This is emphasised by the suggestion that spotted dogfish and seals are amongst the common predators of L. depurator; these species are unlikely to be distracted by the simple autotomy reflex.

2-3.7 SOCIAL BEHAVIOUR

Very few social interactions were recorded during the course of this study. Under most conditions crabs appeared to tolerate the presence of others even under high local densities (> 4 crabs/m^2). In addition, crabs were observed feeding in the presence of other non-feeding crabs with no aggression or interference being provoked. Aggressive interactions were defined as occasions when one or both individuals ceased to move and behave at random with relation to one

another and where a series of approaches or postures led to ultimate retreat or collapse of one interactant. Such reactions rarely occurred spontaneously but were often provoked during attempts to capture crabs for tagging. These interactions were induced by escape from the divers causing a crab to move rapidly towards a conspecific. On all such occasions the stationary crab responded to the approach of a conspecific by raising its body up from the substrate and extending the chelipeds upwards and outwards into a full meral display (Figure 4.11) simultaneously both swimming legs being raised and extended, exposing the vivid markings on the dactylus. In response to this, the approaching crab either moved rapidly away from the stationary crab or formed a similar display. Hazlett (1975) also found that the hermit crab Clibanarius tricolor reacted in a vigorous manner to a rapid approach but the reaction distance was smaller and reaction less vigorous to a slow approach. However, unlike Hazlett's study, interactions between L. depurator were not necessarily won by the initiator, but more usually by the larger crab. These findings are presented in a qualitative, not quantitative, manner as they were obtained incidentally and usually occurred while other information was being gathered. In all these interactions, the encounter was brief but although artificially induced, they provided useful background information on the agonistic behaviour of L. depurator in the field.

On seven separate occasions, pairs of naturally interacting crabs were encountered. The interactions were observed to completion before capture of the crabs for tagging and measuring. Table 2.8 shows the size and sex of the crabs involved in each interacting pair. All interactions involved large adult crabs and occurred during

Table 2.8 Size, sex, and tagging status of crabs involved in social interactions.

	Date of interaction	Sex	Carapace width (mm)	SDI	Tagging status	Outcome
1	Sept. 1981	M	60	0.16	Previously tagged	Winner
		M	50		Not tagged	Loser
2	Sept. 1981	M	55	0.18	Not tagged	Winner
		F	45		Not tagged	Loser
3	Oct. 1981	M	60	0.03	Not tagged	Winner
		M	58		Previously tagged	Loser
4	Oct. 1981	M	55	0.09	Previously tagged	Winner
		M	50		Previously tagged	Loser
5	Nov. 1981	M	48	0.12	Not tagged	Winner
		M	42		Not tagged	Loser
6	Nov. 1981	M	60	0.08	Not tagged	Winner
		M	55		Not tagged	Loser
7	Nov. 1981	M	65	0.38	Not tagged	Winner
		M	40		Not tagged	Loser

September and November, the period during which peak abundance was recorded (Figure 2.19). Difference in size between interacting crabs was generally small although in one case the size difference index (SDI) was 0.38, indicating a large size differential between the crabs. The size difference index was calculated as follows:

$$SDI = \frac{\text{(Size of larger crab) - (size of smaller crab)}}{\text{(Size of larger crab)}}$$

Four crabs carried tags during the interactions and only one of the fourteen interactants was female.

Six of the seven interactions involved static displays by both crabs of the type shown in Figure 4.11. Completion of the interactions was signalled by retreat of the smaller crab in each encounter. During retreat the full meral display (Figure 4.11) was maintained until a distance of approximately 30 cms separated the crabs. Both then returned slowly to normal positions (Figure 4.18) and behaviour.

Interaction number 6 (Table 2.8) however did not follow the same pattern as the other six interactions. A period of static display (Figure 4.11) 15 cms apart, was followed by a slow approach by the smaller crab towards the larger crab. Both crabs maintained the full meral display (Figure 4.11) during this phase. When the distance between the crabs had closed to approximately 10 cms, the larger crab lunged towards the approaching crab and struck it with both chelipeds. The smaller crab then retreated rapidly, still maintaining the full meral display. The larger crab did not follow the retreating crab but remained static in the position shown in Figure

4.14. During the active phase of the interaction, the swimming legs of the lunging crab were waved rapidly backwards and forwards asynchronously over the carapace. The swimming legs of the retreating crab remained in the position shown in Figure 4.11 at all times.

In only one other interaction were movements of the swimming legs observed. In interaction no. 1 (Table 2.8), bursts of swimming leg movements occurred during the stationary display. Only the larger crab carried out these movements, and involved slowly waving one swimming leg backwards and forwards over the carapace. Each burst of movement lasted 4-5 seconds and included approximately one full cycle (forwards and backwards) per second. Two such bursts of movement were made by the right swimming leg and one by the left swimming leg during the course of the interaction. Each burst was followed by a period of static display (Figure 4.11). Approximately 5 seconds after the third burst of swimming leg movement, the smaller crab retreated.

No information concerning length of interaction was obtained, as in all seven cases, the interaction had already commenced when the animals were first observed. However, these results provide an excellent basis for the study of similar aggressive interactions in the laboratory.

2-4 CONCLUSIONS

The overall aim of this study was to plug a gap in our current knowledge and to provide a description of the behaviour and lifestyle of L. depurator in the field and to answer the following specific questions as a necessary preliminary to subsequent laboratory experiments.

1. What is the pattern of habitat use by L. depurator?
2. What are the local population densities?
3. Are local populations stable or do populations and individuals constantly change?
4. Is there any evidence of long term site attachment and, if not, what form do the movements of individuals take?
5. Are local populations uniform in composition or is there evidence of size or sex class aggregation?
6. How do individuals forage and what food items are taken?
7. Are there any breeding population cycles?
8. What form do social interactions take?

The results show that L. depurator does not settle at random with respect to substrate type. Significantly more crabs than would be expected from the relative distribution of substrate types, were found in open exposed areas. This trend was not subject to seasonal variation. The majority of those crabs in exposed areas were observed standing upright in an 'alert' position and it is suggested that this type of habitat utilisation is associated with feeding and anti-predator behaviour.

Population density varied with time within the study areas but during periods of peak abundance, densities of up to 1 crab/7m^2 were recorded. This value is quite low compared to other studies on crustaceans but within the areas in question crabs were aggregated and local densities could be as high as 3.3 crabs/m^2. These values for local density compare favourably with other studies.

Tagging and resight studies show that L. depurator does not show any long term site attachment and that in the area sampled, local populations are not stable in the long term. Individuals within the area are constantly changing but occasionally tagged individuals returned to the study area thereby maintaining a very low level of continuity. Attempts to examine the nature of these individual movements failed to produce any information and it is suggested that L. depurator may show much larger scale movement and migration patterns than was expected. Further studies using more sophisticated ultrasonic tagging and tracking techniques would almost certainly allow the nature of these movement patterns to be examined.

Local populations did not show uniform composition over the course of the study. As with other crustacean species, there was evidence of a seasonal sex ratio biased towards male crabs. Significantly more male crabs were observed during the months of peak abundance in late summer and autumn and this trend continued into early winter. This differential sex distribution is almost certainly caused by either migration of females away from the study area or by seasonal migration of male crabs into the study area.

As discussed above, attempts to gain information concerning the nature of these movements were unsuccessful. However, differential distribution of male and female crabs have been recorded for other species and seem to be related to breeding cycles. It is possible that the movements shown by L. depurator are similar to these other studies, however, further more intensive tagging studies may reveal the true nature of the phenomenon.

Within the study area, L. depurator did not appear to be randomly distributed and the majority of crabs were found within 1 metre of the nearest conspecific. This apparent clumping was not caused by single sex groupings and was most likely a reflection of localised food or shelter.

Studies on food and feeding behaviour were through simple observation. It is likely therefore that the description of food items which L. depurator was observed taking is an underestimate of all possible food items. However, L. depurator was observed to take a wide range of items and in common with many other crustaceans was shown to be essentially a predator of slow moving benthic macro-invertebrates. In addition, however, L. depurator was also shown to be capable of taking larger, more active prey, such as small fish and cephalopods. The value of direct underwater observations are clearly illustrated in this area.

Investigation into breeding and population cycles showed that ovigerous females are observed in two distinct phases between April and September while recruitment occurs primarily between April and May. The increase in the adult population four months later was not

due to this period of recruitment but was due to movement of large size/class individuals into the area. Again, further tracking of individuals may elucidate the movements causing fluctuation in population abundance.

No naturally occurring predator-prey interactions were observed in the field; however, three different types of escape response were shown to approaching divers and these may represent the range of responses shown to natural predators in the wild. These responses include an instant burial response, shown only by juvenile crabs; a zig-zag or protean response shown mainly by large crabs; and a cover response shown by all types of crab. It is postulated that these responses have distinct survival value, allowing crabs to forage on exposed areas while also allowing escape from predators.

Very few spontaneous social interactions were observed in the field even where local density was high or where individuals were feeding in the presence of non-feeding conspecifics. The low levels of intraspecific aggression may in part be explained by the disturbing effect of the divers; however, the seven separate interactions which were observed, continued to completion with little notice being taken of the divers. It appears, therefore, that levels of aggression are low. Each interaction was fully documented and these results provide a valuable basis for the study of similar interactions in the laboratory. Again in this area, the value of direct underwater observation is clearly illustrated.

The results outlined above by no means provide a definitive account of the behaviour and lifestyle of L. depurator in the wild. It deals

only with one locality and it is inevitable that aspects of the behaviour and ecology will vary with local environmental and topographical conditions. However, while further study is undoubtedly required in certain fields, the present study provides a general background account of the biology of L. depurator and the value of this to the design of subsequent experiments and interpretation of data is considerable. In addition, the current study extends our knowledge of the crustaceans and while L. depurator is of no commercial interest at present, it is closely related to a species which is currently important in this respect, L. puber. In light of this, L. depurator may become a candidate for limited fishery exploitation in the future. Furthermore, L. depurator is sympatric with and possibly in competition with other commercially important species, such as Nephrops. Therefore, as well as providing a general background account, the present study provides valuable comparative information and also information which may have implications for the study of other important species.

2-5 SUMMARY

1. Regular field observations using SCUBA techniques were made at two sites in Loch Sween (Argyllshire) in an attempt to describe the behaviour and ecology of L. depurator as a background for subsequent laboratory studies.

2. Abundance of animals varied over time with peak abundance occurring during the months of September-November corresponding to periods of warm water. Local variations in visibility did not seem to affect local abundance.

3. During periods of peak abundance, densities of 1 crab/7m^2 were observed but average density was much lower at 1 crab/25m^2.

4. There was some evidence for migration from the study site, similar to that reported for other species. Transect studies failed to yield any information on these movements and it is postulated that further studies using ultrasonic tagging and tracking techniques may elucidate the movement patterns of individuals.

5. Claw tagging of individuals with Floy Co. Spaghetti Cinch-Up tags revealed that there is very little long term site attachment by L. depurator at Loch Sween. Individuals within the study area were continually changing even though in the short term, local abundance remained relatively constant. A very low level of

continuity was maintained within the study area by tagged individuals returning periodically. It is postulated that this is of little significance due to the low level of continuity.

6. During summer months local populations were found to be biased in favour of male crabs. Transect studies failed to identify differential female/male migration and again it is suggested that further tracking studies using ultrasonic tags may be needed to elucidate these movements of individuals.

7. Individuals were most commonly observed within 1 metre of the nearest conspecific and localised densities of up to 3.3 crabs/m^2 were reported. These local aggregations did not appear to be formed by single sex groups.

8. Ovigerous crabs were observed in two distinct phases between April and September. This observed brooding period is substantially different from that reported in some studies and similar to others. It is suggested that this may reflect inadequate sampling of certain areas and the brooding period of L. depurator may be longer than previously stated.

9. Recruitment of juvenile crabs occurs in early spring but the subsequent increase in adult crabs is caused by movement of large crabs into the study area, not by growth and maturation of the early spring immigrants.

10. Habitat utilisation by L. depurator appears to be non-random at Loch Sween. Crabs were most commonly found totally covered

or alert and standing in exposed areas. It is suggested that this habitat utilisation is associated with feeding and anti-predator behaviour.

11. Observations on food and feeding behaviour showed L. depurator to be essentially a predator of sessile or slow moving benthic macroinvertebrates, a diet similar to that of many larger crustaceans. However, L. depurator also has the ability to capture larger active prey through its ability to swim at great speed.

12. L. depurator showed three main types of escape response to approaching divers and these were taken as normal anti-predator responses. The adaptive significance of each of the responses is discussed.

13. The incidence and possible causes of physical damage shown by crabs in the field is discussed. Levels of physical damage in the field are lower than those observed in laboratory populations, probably due to lower density of crabs in the field.

14. A number of naturally occurring social aggressive interactions were observed in the field. These interactions were described and the results provide a basis for the study of similar aggressive interactions in the laboratory. The observed incidence of such aggression in the field was very low.

CHAPTER 3

AN INVESTIGATION INTO LOCOMOTOR ACTIVITY PATTERNS

IN *LIOCARCINUS DEPURATOR*

3-1 INTRODUCTION

All living organisms inhabit a world in which there are a number of geophysical oscillations such as tidal, diurnal, lunar and seasonal rhythms. In many animals, this external rhythmicity may be mirrored by physiological, electrochemical, biochemical and behavioural rhythms ranging in frequency from rapid oscillations of spike output of the nervous system, through pulse rate and daily cycles, to much longer population cycles.

Cyclic phenomena have received considerable attention, with interest being shown both in the mechanism by which these rhythms are produced, and in their adaptive significance. The large body of literature on cyclic phenomena may be divided into a number of categories (Naylor and Hartnoll, 1978) but for the purposes of this study, only rhythmic locomotor activity will be considered, with particular attenton being paid to the crustacea.

The intertidal crabs of the genus Uca were the first crabs in which a clear tidal locomotor rhythm was shown to exist. Brown, Brown, Webb, Bennett and Schriner (1956) and Bennett, Schriner and Brown (1957) studied the locomotor activity of U. pugnax. Crabs were maintained individually under constant conditions, away from the direct influence of the tides. Under these conditions, the crabs displayed rhythmicity for about 10 days. Individual responses varied but the population data displayed a clear cut tidal activity rhythm, with peak activity occurring 3-5 hours before the time of maximum low tide. Improved maintenance techniques for fiddler crabs enabled

Barnwell (1966) to record tidal locomotor rhythms lasting nearly a month under constant conditions in U. pugnax and U. pugilator. These findings were confirmed by Atkinson and Naylor (1973) for U. pugilator.

Two species of Brazilian fiddler crabs, U. maracoani and U. mordax were shown to exhibit similar tidal rhythms when held in groups under constant conditions (Barnwell, 1963). However, U. mordax collected from the Caribbean shore of Costa Rica where there is only one tide per day, showed only this diurnal frequency, when held in the laboratory under constant conditions. Barnwell (1968) transplanted these animals to the opposite side of the 110 mile wide continent and exposed them to the twice per day tides encountered on the Pacific coast, by placing them in holding cages on the shore. Subsequently, when transferred to constant conditions in the laboratory, some crabs exhibited a twice daily tidal rhythm. Similarly U. minax, exposed to one tide per day in the Mississippi basin express only a diurnal rhythm in the laboratory under natural light/dark (LD) conditions. As with U. mordax, exposure to twice daily tidal rhythms soon result in U. minax acquiring a rhythm phased to the new tidal regime.

Many other intertidal crustaceans have also been shown to exhibit strong tidal locomotor rhythmicity. The Californian amphipod, Synchelidium emerges from the sand to feed in the surf at the peak of each high tide. As the tide recedes, the crustaceans return to the substrate. The persistence of this behaviour, recorded as spontaneous activity in constant conditions in the laboratory was studied by Enright (1963). A clear tidal (12.4 hour) rhythm lasting for about 3 days was found. The first two peaks mimicked the tides of the

original habitat but then deviated progressively, the interval between comparable daily peaks becoming considerably longer than the expected 24.8 hours. Almost identical rhythms have been reported for the amphipods Corophium volutator (Morgan, 1965), Orchestia mediterranea (Wildish, 1970), Bathyporeia pelagica (Fincham, 1970), B. pelosa (Preece, 1971) and Marinogamarus marinus (Fincham, 1972); the isopod Eurydice pulchra (Jones and Naylor, 1970) and the prawns Palaemon elegans and P. serratus (Rodriguez and Naylor, 1972).

Carcinus maenas, the common shore crab has also been studied extensively and the investigation of locomotor activity and its control has been carried much further than for most other species due to its wide distribution and ease of collection. Although Carcinus may be found to a depth of 60 metres (Allen, 1967), it is essentially an intertidal species. Under constant conditions in the laboratory, activity is strongly rhythmic (Naylor, 1958) with peaks corresponding to time of expected high tide. Night-time tidal peaks are larger than day time peaks suggesting a superimposed circadian component, and under constant conditions these rhythms lasted 6-7 days. Naylor (1960) also showed that wild caught Carcinus isolated from tidal effects, but housed under natural light/dark cycles, exhibit tidal rhythms. However, after a period of 4 weeks this frequency completely disappears, with activity becoming nocturnal. Williams (1969) showed that the tidal rhythm of the crab Hemigraspus edwardsii also disappeared after a time in the laboratory. In experiments with Carcinus collected from sites with little or no tidal range (Naylor; 1960, 1961) crabs showed only circadian rhythms. Further studies with juvenile Carcinus reared from eggs in the laboratory showed that tidal rhythmicity did not depend on prior exposure to natural cycles of the tide (Williams and Naylor, 1967).

As with many other decapods, there is strong evidence to suggest that rhythm in Carcinus is regulated by factors in the eyestalk (Arechiga and Naylor, 1976). Bilateral eyestalk ablation induces arhythmic hyperactivity (Naylor and Williams, 1968) which may be reduced by injection of eyestalk tissue (Naylor and Williams, 1968; Naylor, Smith and Williams, 1973; Williams, Pullin, Williams Arechiga and Naylor, 1979). This indicates that eyestalk secretions are important factors in the control of rhythmic behaviour. The histology of eyestalks of active and inactive crabs was investigated by Williams, Pullin, Naylor, Smith and Williams (1978) in an attempt to relate activity to neurosecretory cycles. Their results showed that one of the six neurosecretory cell types in the optic peduncle of Carcinus exhibited cytoplasmic changes which correlated with the tidal rhythm of locomotor activity. Similar cyclic changes in neurosecretory cells, also possibly correlated with the locomotor rhythm, occur in the corpora allata of Drosophila melanogaster (Rensing, 1964).

In addition, the locomotor activity patterns of crabs following heat cautery of selected regions of the optic peduncle were investigated in an attempt to locate the sites of release of the proposed neural depressing hormones. They concluded that with Carcinus it was unlikely that the clock control depended ultimately on only one factor, but that a combination of neuro-electrical and neuro-hormonal rhythms was involved.

The examples of rhythmic locomotor activity cited above concern littoral crustacea. However, other groups of animals have also been studied and comparison of results may provide information

concerning the adaptive significance of the rhythms shown. In the wild, the shanny Blennius pholis feeds in the high tide zone and rests in pools in the low tide zone. Consequently, it migrates between feeding and resting grounds with each flood tide. In the laboratory, recordings under constant conditions showed a clear tidal locomotor rhythm which persisted for at least four days before damping out (Gibson, 1965). Analysis of the rhythm showed that no endogenous diurnal component existed (Gibson, 1967). Further experiments however showed that fish held in natural light/dark (LD) cycles, exhibited a strongly marked exogenous component in which daytime activity was much higher than activity during darkness (Gibson, 1971). The influence of light and darkness on the activity of B. pholis is strong, even in the early life of the fish. Quasin (1955) found that the larvae only fed during periods of illumination and remained motionless during periods of darkness. Suppression of activity by darkness also occurs in the adult and is expressed as a diurnal component in the tidal rhythm.

A double peaked circadian pattern of activity has also been described in B. gattorugine from the Meditterranean (Gibson, 1969) where in the absence of tides, cycles of light and darkness are the most regular fluctuating stimuli. It seems that B. pholis in non-tidal conditions can regulate its activity in a similar manner, but Gibson (1971) suggested that on the shore where the tides dominate the life of B. pholis, the accompanying cycle of hydrostatic pressure is the most effective stimulus for keeping the activity of the fish correctly in phase.

Comparing the properties of the rhythms of Carcinus as described by Naylor (1958, 1963) and Williams and Naylor (1969) with those of the rhythm of B. pholis (Gibson, 1971) is of interest. Both animals are found in the same environment but the properties of their rhythms differ in some respects. In freshly caught animals, both species exhibit strong tidal rhythmicity, but Carcinus has an endogenous 24 hour component which causes it to be more active on night tides. The tidal rhythm of B. pholis on the other hand is modified directly by light and tidal peaks occurring during darkness are smaller than those during daytime. These different patterns of activity represent different adaptations to life in a similar environment. Carcinus being relatively slow moving would represent an easy prey item to any sea-bird or predatory fish, should the crab be active during daytime high tides. Increased activity during night time high tides however, may allow Carcinus to feed with a reduced risk of predation. B. pholis, while also suffering similar predation to Carcinus is much more agile, and as such may be more adept at avoiding predators. In addition, B. pholis relies more heavily on vision for feeding than does Carcinus; consequently increased activity during daytime high tides may allow B. pholis to feed while still avoiding predation.

Rhythmic locomotor activity is not restricted to animals from the littoral zone. The sub-littoral crab, Goneplax rhomboides burrows in mud (Rice and Chapman, 1971; Atkinson, 1974), its burrows frequently being found in the vicinity of Nephrops burrows. Under constant conditions in the laboratory these crabs display a persistent circadian rhythm of nocturnal activity (Atkinson and Naylor, 1973) with animals returning to their simulated burrows for 'expected' daytime.

Atkinson (1974) suggested that this activity rhythm allowed crabs to leave their burrows at a time when they could feed in optimum light conditions without excessive danger of predation. However, Atkinson (1974) also suggested that Goneplax from different depths may be active away from their burrows at different times, being day active in deep water where light intensity is low and night active in shallow water where daytime light intensity is high. Support for this was obtained by Farmer (1974) who trawled more Goneplax during the day than night from deep water.

The occurrence and control of any rhythmic activity is of considerable theoretical interest but when the species involved is of commercial importance, they are of practical value as well, with implications for the management of fished populations. For these reasons, Nephrops has received extensive study. Oakley (1978) reported bimodal peaks of Nephrops catches, in agreement with the data of O'Riordan (1964), Hillis (1971), Farmer (1976), Arechiga and Atkinson (1975) and Garrod (1976). He suggested that changes in availability of Nephrops to trawls was related in a complex manner to circadian rhythms of burrow occupancy by the prawns which in turn was related to their foraging behaviour and responses to light (Atkinson and Naylor, 1976; Hammond and Naylor, 1977). The activity of Nephrops away from the burrows was shown by Chapman and co-workers (1971, 1972, 1975) to vary with depth, with peak activity at night in shallow water (30m), daytime activity in deep water (100m), and two peaks around dawn and dusk in intermediate depths. Chapman et al (1975) proposed that the emergence of Nephrops from their burrows was confined to a narrow range of light intensity, accounting for the above results. However, Arechiga and

Atkinson (1975) recorded very little change in bottom light intensity in the interval between peak catches, indicating that increased light levels could not normally be responsible for the observed variation in catches. They also showed that the level of illumination during periods of suppressed catch in winter was more than 10 times lower than that at the same time in summer. These variations suggested that actual light intensity may not have been the most important factor controlling activity and Atkinson and Arechiga (1975) proposed that change in light level may be a more reliable cue.

Laboratory studies have shown that rhythmicity of Nephrops catch is not determined by an endogenous rhythm of emergence and time spent away from the burrow. However, Nephrops does show an endogenous rhythm of activity with peaks occurring during subjective night (Arechiga and Atkinson, 1975; Atkinson and Naylor 1976; Naylor and Atkinson, 1976). Atkinson and Naylor (1976) showed that the endogenous nocturnal rhythm was expressed most strongly within the burrow, although the lobsters vacated the burrow frequently. They therefore suggested that the activity rhythm in laboratory individuals was primarily burrow orientated, connected with burrow excavation and maintenance. The evidence therefore suggested that low Nephrops catches at night were due to strong burrow orientated behaviour which resulted in low availability of the majority of the population to trawls.

Oakley (1978) suggested however, that the variation in daytime catch reflected a pattern of feeding behaviour in the population, with animals which had not fed since the previous day leaving their burrows at dawn in response to increasing light levels. The animals

subsequently forage before returning to burrows to consume the food items, the inter-excursion period being determined by the amount of food taken. At dusk the endogenous rhythm of burrow-orientated behaviour is expressed again, resulting in low availability of prawns to the trawls at night time. In this case, the practical importance of carrying out both laboratory and field work is clearly illustrated.

The present study concerns the sub-littoral swimming crab, L. depurator. This crab has been reported from 5m (Walker, 1892) to 220 metres (Greig, 1927) on sand, muddy sand and gravel (Allen, 1967) and is oftern found in the same areas as Goneplax and Nephrops. Unlike Goneplax and Nephrops, L. depurator does not construct and live in burrows, but individuals may be found totally buried in the substrate with only the eyestalks protruding. It is possible that this behaviour serves a similar protective function to that of the more fully developed burrowing behaviour of Nephrops and Goneplax. Considering the similarity in life styles between Nephrops, Goneplax and L. depurator and considering the large number of marine animals which show rhythmic locomotor behaviour, it is reasonable to suspect that L. depurator may also show rhythmic activity patterns. The presence of any such activity rhythm may influence much of the other behaviour of the crabs. Therefore, for a full understanding of the causes of any behavioural change shown by L. depurator, it is important to investigate the presence or absence of cyclic locomotor activity.

The study described in this chapter was therefore designed to answer the following questions, and to provide important information for the planning of subsequent experiments.

1. Does L. depurator show cyclic locomotor activity when held under standard light/dark (12:12 LD) laboratory lighting conditions?
2. If such cyclic activity exists, is it an artefact caused by a cyclic laboratory environment, or is it endogenous?
3. What is the frequency of the cycle of locomotor activity?
4. Do crabs from different localities exhibit similar activity patterns?

All animals used in this section were collected during spring/summer.

3-2 MATERIALS AND METHODS

3-2.1 SAMPLING

Animals used in this study were collected from three sites. The Isle of Cumbrae (Firth of Clyde), Loch Sween (Argyllshire) and Loch Feochan (Argyllshire) - (Figure 2-1). Specimens obtained from the Firth of Clyde were collected by dredge from a depth of >30 metres and transported by rail to the University of Glasgow. Rail transport, however, proved unpredictable with many specimens in poor condition on arrival in Glasgow. For this reason, animals were collected from Loch Sween or Loch Feochan whenever road transport was available. Specimens from these sites were collected from a depth of 3-9 metres by SCUBA diving, transferred to polystyrene containers and transported direct to Glasgow by road.

Prior to placement in the experimental tank, the sex and size of each crab was noted. Size was measured as carapace width (mm). Crabs were placed in the experimental tank directly on arrival in Glasgow and were not fed during the course of the experiment. Crabs showing any evidence of ill health or poor condition may well also show modified or abnormal behaviour patterns. Three signs of unsuitable condition were used.

1. Crabs in moult or immediate post-moult condition.
2. Crabs with missing limbs.
3. Crabs with heavy encrustment of the cuticle.

Any crabs showing one or more of these conditions was not used in this study.

Only one set of recording apparatus was available, allowing only one crab to be studied at any point in time. Consequently, the sample size reported in this study is lower than that of other more intensive investigations in which large numbers of actographs are used simultaneously. However, study of activity rhythms is not the sole aim of this thesis and the sample size is sufficient to allow the previously stated aims of this Chapter to be achieved.

3-2.2 ACTIVITY MONITORING

Many early investigations into activity rhythms used simple tipping actographs. In these, each time an experimental animal crossed a central fulcrum, the aquarium tipped activating a microswitch. This type of apparatus however, can lead to an underestimate of activity, as activity at either end of the actograph remains undetected. More recent studies have greatly improved on the early equipment, with activity being recorded by the interruption of a series of light beams impinging on light activated switches. The early tipping actographs were analagous to a system with only one central light beam. A series of light beams is a much more sensitive system, if information from each light beam is recorded and stored separately. In this way an estimate is obtained not only of level of activity, but also of the position of the animal within the apparatus at any point in time.

Since the daily pattern of locomotor activity of some crustacean species may be influenced by the type of apparatus used to record their movements (Atkinson and Naylor, 1973), the design of an actograph is important (Bregazzi and Naylor, 1972). In the present study, each crab was placed in a large glass aquarium (60 cm x 30 cm x 38 cm) with a 2 cm deep layer of sand and mud. Preliminary experiments were carried out in an isolated aquarium with oxygenation provided by airstone and filtration by Eheim pump, however, all experimental crabs were housed in an aquarium connected to a circulating sea-water system. No in-tank aeration was required with this system, thereby removing a possible source of disturbance to the crabs. Fresh seawater was fed slowly to the aquarium through a narrow gauge inlet pipe, thus preventing large water movements and removing another possible source of disturbance. The seawater was monitored and maintained between 10 and 12°C, with a salinity value of 33% . The experimental tank was placed in a laboratory in which access was limited to the experimenter, but after introduction of experimental animals, the tank was completely screened as an added precaution. A small observation port (6 cm x 3 cm) was left in the screen, allowing periodic checks of both animals and equipment. The experimental apparatus is shown in Plate 3.1. Six light beams were directed across the tank onto 15 volt light activated switches. These in turn were connected to an 8 Channel, Rustrak Event Recorder, with each light beam corresponding to a particular channel of the event recorder. Each time a light beam was interrupted a recording pen was deflected on the channel corresponding to that light beam. In this way the position of the crab in the tank could be determined at any point in time. Data from each channel was stored separately as well

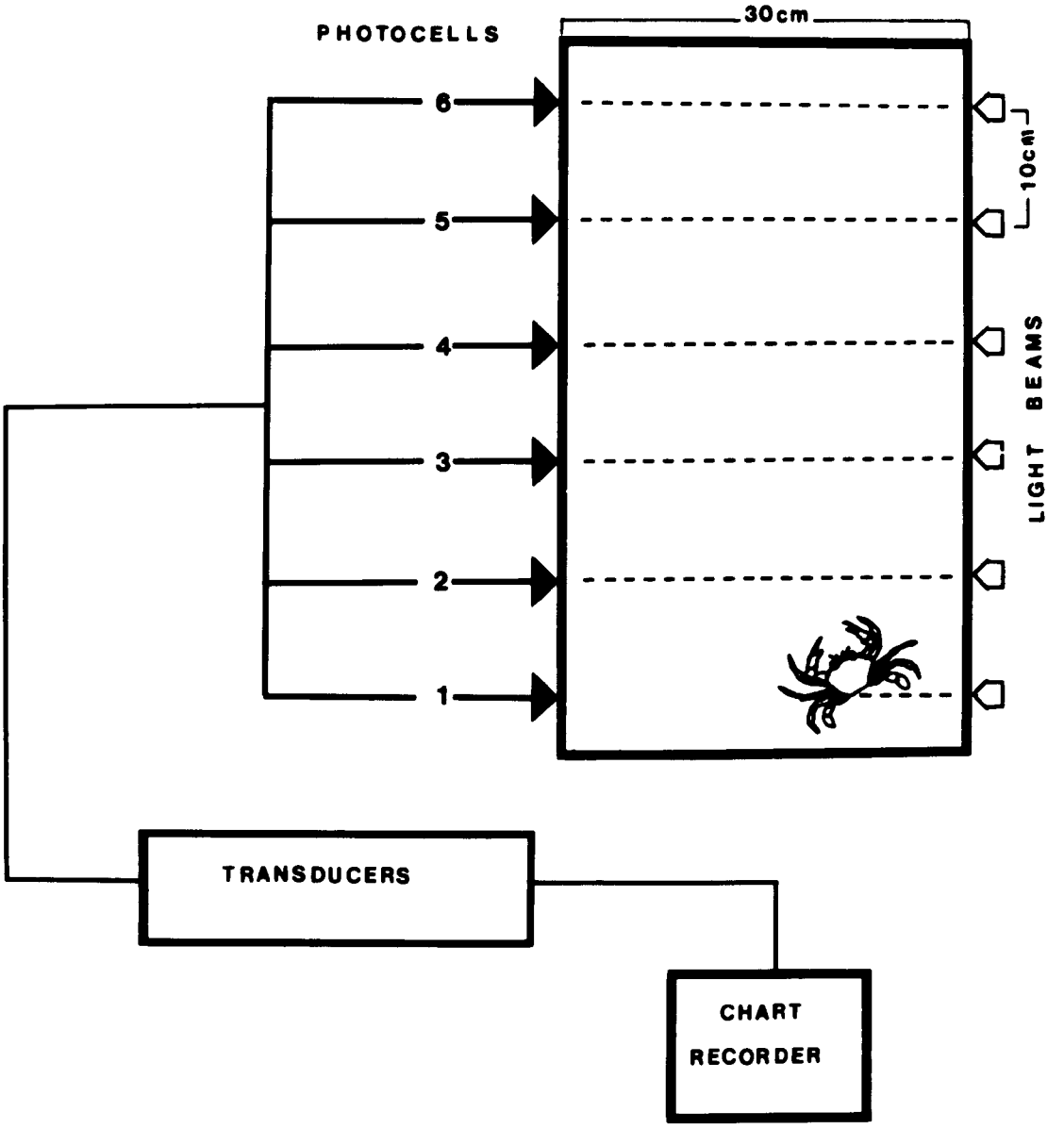


Plate 3.1

Plan diagram of apparatus used to record locomotor activity shown by L. depurator in the laboratory.

as being totalled and used as an indicator of overall activity. The event recorder was geared to a recording speed of 38 cm per hour, a rate allowing reasonable economy while permitting identification of all but the most rapid of individual movements. The light beams were arranged at a height of 15 mm above the sediment and spaced at 100 mm intervals. As the crabs used in this study were of a size range 32-60 mm (carapace width), this light beam spacing enabled all but the smallest movement along the tank to be detected. Similarly, the height of the beams prevented undetected passage underneath. L. depurator raises its body off the substrate when walking. The smallest crabs used in this study reached a height of greater than 15 mm when raised off the substrate. Consequently, no crab was capable of passing below a light beam, except by burrowing. Burrowing through the substrate was never observed in the laboratory.

Light beams were produced by Vickers microscope lamps which enabled a narrow, low intensity beam of light to be focused directly onto the light activated switches. A spot of only 7mm x 7mm falling on the light activated switches was possible using this equipment.

Atkinson (1974) found that Goneplax displays consistent, clear cut rhythmicity only when in actographs provided with tubes to simulate burrows. Similarly, Arechiga and Atkinson (1975) designed an actograph with a simulated burrow to study the movement of Nephrops. L. depurator, unlike Nephrops and Goneplax, does not actively build burrows in which to live. However, L. depurator is commonly found on, or partially submerged in, the same type of muddy sediment as Nephrops and Goneplax. Therefore, in an attempt

to provide as natural an environment as possible, a 20mm layer of this muddy substrate was provided in the experimental tank. Preliminary experiments however, suffered similar problems to those encountered by Atkinson (1974) in a study of activity rhythms in Goneplax. When the fine muddy sediment was disturbed by the experimental animals, clouds of silt reduced the efficiency of the photocells. The result from these preliminary experiments in which clouding occurred were discarded and to counter this problem, the mud sediment was replaced by a sand substrate in the current study. This removed the clouding problem and did not appear to affect the behaviour of the crabs. In many areas, L. depurator may be found on sandy subtrates, and as such, the conditions in the experimental tank were felt to be as close to those of the natural environment as possible.

3-2.3 SPECTRAL SENSITIVITY

Investigation of the spectral sensitivity of a number of decapod crustacean species indicated that sensitivity is extremely low at wavelengths of 700 nm (red light) and above, (Kennedy and Bruno, 1961; Waterman, 1961; Scott and Mote, 1974) and that maximum sensitivity of benthic crustaceans are in general in the green/yellow range of the spectrum (520-570 nm). In addition, there is an increasing volume of evidence supporting the hypothesis that the sensitivity of the visual organs of aquatic animals, particularly decapod crustaceans and fish, is closely correlated with photic conditions in the animals natural environment, (Munz, 1965;

Fernandez, 1973; Hindley and Penn, 1975). These observations, together with the low transmission of red radiation through water, suggest that marine decapods such as L. depurator are unlikely to be sensitive to long wavelength red and infra-red illumination. For this reason, red filters (Kodak Wratten gel, number 25 red) were placed in front of the light sources in this study. During preliminary studies, L. depurator was shown to have some sensitivity to the red light showing orientation responses to a moving object when maintained under red illumination only. However, the behaviour of the crabs did not appear to be affected by the narrow, red light beams, consequently this apparatus was used throughout the present study.

3-2.4 DETECTION OF SWIMMING ACTIVITY

Light beams arranged at a high level in the water column in order to detect crabs engaged in swimming behaviour were not used. Extensive preliminary observations indicated that singly housed crabs rarely exhibited swimming behaviour, most crabs remaining on the substrate at all times. In addition, any such behaviour could be detected from the paper trace produced by the event recorder. Swimming behaviour as shown in figure 3.3 was observed on only four occasions throughout the entire study. In figure 3.3, activity recorded on channel 4, for example, followed by activity on channel 2 with no intervening activity on channel 3 suggests that the crab has passed over the light beam by swimming. The time scale of events between activity on channel 4 and activity on channel 2 is of the order of a few seconds. This indicates a simple swimming hop rather

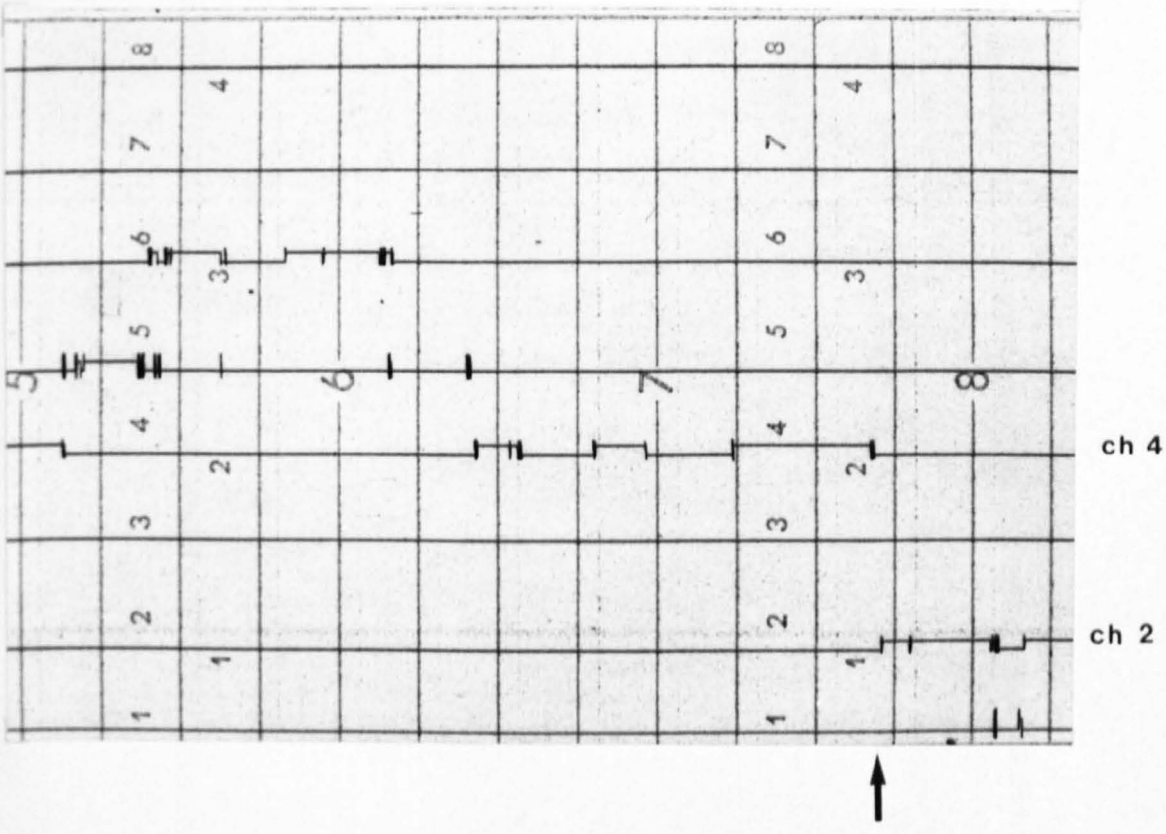


Figure 3·3
Photograph of raw data trace showing an example of swimming activity between channels 2 and 4. Vertical arrow indicates point of occurrence of swimming activity.

than a more protracted bout of swimming. All four instances of swimming behaviour observed, followed this swimming hop pattern.

3-2.5 ACCLIMATISATION

Hazlett (1966) has shown that the immediate past of an individual hermit crab can affect its behaviour in the present. For this reason, Elwood and Glass (1981) allowed a 16-18 hour acclimatisation period between experimental manipulation and observation, in a study on hermit crab shell-fighting behaviour. Recent investigation (Morris and Taylor, Glasgow University, Pers.Comm.) has shown that the heart rate of the prawn Palaemon elegans requires a period of 6-8 hours to return to normal after experimental manipulation. Taylor (1977) however, has shown that Carcinus may require periods of up to 24 hours in which to recover after experimentally induced stress and Taylor (Pers. Comm.) suggests a period of 24 hours may be necessary for most crustaceans to return to normal after manipulation. In this study, crabs were allowed 24 hours in which to acclimatise after introduction to the experimental tank. This acclimatisation period served two purposes; it allowed crabs to recover from the stress induced by collection and handling and it allowed them to become familiar with the lighting regime and conditions in the novel environment of the aquarium.

The literature on this subject however, is sparse, and most of the studies concentrate on recovery of physiological systems only. Therefore, to check the validity of using 24 hours as a sufficient

acclimatisation period for L. depurator, locomotor activity was recorded throughout the acclimatisation period for a number of crabs and compared with subsequent activity. This was carried out to ensure that atypical locomotor activity caused by experimental manipulation was not included in subsequent analysis. After acclimatisation, all animals were maintained under experimental conditions for a period of 5 days and 8 hours unless otherwise stated (Table B.1). This gives a sampling period of 256 (2^8) intervals and Fourier algorithms are generally most efficient when the number of sample periods is an integer power of 2 (Lynn, 1973).

3-2.6 LIGHTING REGIMES

In a study of some effects of light on locomotor activity in Nephrops, Arechiga and Atkinson (1975) maintained animals in a constant temperature room in which diffuse green light was used. A wavelength of 530 nm was chosen because it was within the range of greatest penetration through coastal seawater (Holmes, 1957; Kain, 1966) and also was within range of maximum absorption for visual pigments in related crustacean species such as the lobster Hommarus americanus (Wald and Hubbard, 1957). This was an attempt to produce a natural environment and in some of their experiments, the lamps were driven by a photocell which monitored external illumination and thus produced a waveform which roughly paralleled the natural light/dark (LD) cycle. Precisely regulated systems similar to this, which mimic natural conditions, are important when attempting to understand the factors controlling locomotor behaviour

in the field. The present study was designed primarily to study locomotor behaviour patterns shown in the laboratory, as a preliminary to further laboratory experiments. For this reason, no attempt was made to mimic the natural environment of L. depurator in terms of light quality or light intensity. Water quality and sediment type however, were maintained as close as possible to natural conditions in order to create a realistic, if not totally natural environment.

Three main lighting regimes were employed during this study.

1. Standard laboratory light/dark regime (LD 12:12)
2. Constant illumination (LD 24:00)
3. Constant darkness (LD 00:24)

Under the standard laboratory light/dark regime, 12 hours of constant illumination was followed by 12 hours of constant darkness (LD 12:12). In regimes 1) and 2) illumination was provided by fluorescent tubes, colour balanced for daylight, with a light intensity value of 13.3 (read by Sangamo Weston V light meter) at the surface of the tank. In Regime 1), lighting was controlled by timer switch ensuring automatic and consistent control of lighting conditions. Transition between light and dark states was abrupt.

Each crab was given an experimental identification number and this identification is given on each plot shown in this Chapter. Crabs held under 12:12 conditions were given the prefix D, crabs held under LD 24:00 were given the prefix TØ, while crabs held under LD 00:24 were given the prefix TD. For a full list of experimental parameters for each crab see Table B.1 (Appendix B).

3-2.7 3-DIMENSIONAL PLOTTING OF TIME SERIES DATA

Each record was divided into 30 minute sections and the number of breaks of each light beam per 30 minute section was totalled and used as an estimate of activity. An estimate of overall tank activity (Channel Ø) was produced by summation of activity estimates from Channels 1-6. These data were then transferred to computer file for storage and analysis. One such data file is shown in Appendix A. A Digital Corporation PDP-11 computer was used for all analysis in this section.

For each experiment, a plot of activity against time interval number was produced for each of the six light beams in the experimental apparatus. Throughout this section, time interval number indicates the number of 30 minute intervals which have passed since the beginning of the experimental recording. A similar plot of activity against time was produced for Channel Ø. The intermediate process of plotting activity of each individual channel allows a check to be made on non-random use of, or attraction towards certain areas of the tank by any crab. However, in practice, simultaneous scrutiny of plots obtained from each of the six recording channels proved prohibitively difficult and could often lead to an incomplete understanding of the patterns of locomotor activity being displayed by a crab.

In order to overcome this problem and to elucidate the locomotor behaviour shown by experimental crabs, 3-dimensional plots of activity, time and position in tank were produced from each set of experimental data. In these plots, the X co-ordinate represents time,

the Y co-ordinate represents activity and the Z co-ordinate represents the position in the tank where activity occurs. These plots provide a clear and concise representation of activity throughout the experimental aquarium over time. They also allow immediate and easy comparison to be made between activity patterns produced by different crabs and therefore greatly aid the analysis and interpretation of the data.

3-2.8 QUANTITATIVE DATA ANALYSIS

A number of methods of detecting and analysing activity rhythms are available and include the following:-

1. Data plotting with one axis representing time.
2. Moving average or smoothing procedure.
3. Autocorrelation.
4. Schuster type spectral analysis (Periodogram).
5. Fourier transform type spectral analysis of an autocorrelation function (Spectogram).
6. Multiple regression analysis.

DATA PLOTTING

The simplest way to depict time series data is to plot a graph with the X-axis as time and the variate as a function of time on the Y-axis (Broom, 1979). If the time series is long enough and there is little variation in the wavelength of the dominant cycle it is usually possible to determine that wavelength with reasonable accuracy.

MOVING AVERAGE CALCULATION

This is a form of digital filtering (Koopmans, 1974) and involves the calculation of a simple moving average to smooth the data. This smoothing will obscure short wavelength cycles but may allow the dominant periodicity to be described accurately enough to make any further analysis unnecessary.

AUTOCORRELATION

Autocorrelation is simply the correlation of a sample with itself and may be expected to show that a value which is a lag of i intervals after the first interval in a time series is positively correlated with that first value. To obtain an autocorrelation plot, correlation coefficients are calculated for all the possible lags Autocorrelation will pick up dominant regular patterns and is a sensitive method for detecting simple rhythms.

SCHUSTER TYPE SPECTRAL ANALYSIS

This was an early type of spectral analysis described by Schuster (1898) and discussed by Enright (1965a). The Schuster periodogram is similar to the Fourier transform of the sample covariance function and is an approximate estimate of the power spectrum, however, the method assumes that the majority of the variability in the data is provided by the cycle whose presence was originally suspected and around which the calculation is based. A further problem is that multiples of the principle peak will also be shown.

FOURIER TRANSFORM TYPE SPECTRAL ANALYSIS

This involves carrying out Fourier transformation of the auto-correlation function of time series data. The plot of this spectral

density fucntion against frequency gives a measure of the distribution of variance in a time series over a range of wavelengths. This form of spectral analysis is most effective where the recurring pattern is a sine wave and is of particular value because multiple rhythms are readily separated into component cycles. In addition, the statistical significance of peaks can be calculated using an appropriate test based on the X^2 distribution (Campbell and Shipp, 1974).

MULTIPLE REGRESSION ANALYSIS

If multiple cycles are present in a time series, the dominant cycle can be detected by spectral analysis, its contribution to total variance can be assessed using multiple regression and it can then be removed and the residuals further analysed (Box and Jenkins, 1970). Spectral analysis or any other analytical method can then be carried out on the residuals to see if there is evidence of any remaining periodicity (Broom, 1979). This technique has advantages if there are trends in the data on multiple rhythms and it allows the calculation of the statistical contribution of a particular cycle to the total variance in the data.

For a full description and comparison of each of these techniques, see Broom (1979).

The decision as to which analytical method to use for exploratory investigations of an observed time series must depend on the questions asked about the data and the expected complexity of the rhythms (Broom, 1979). The initial step in any analysis however should be the preparation of a plot of activity against time. If the question being asked is whether a cycle of a given frequency is

present and this is clear from the data plot then no further analysis is required. However, if a simple but less obvious cycle is suspected, or more than one cycle is suspected, then one of the other techniques is advisable.

For most biological time series with periodic components, it is desirable to investigate using spectral analysis, perhaps in conjunction with autocorrelation (Broom, 1979). This prompts the question as to which of the types of spectral analysis is adequate. Enright (1965a) describes the use of Schuster-type analysis in detail but considers that it is best used to determine which data sets warrant further analysis and Enright (1965b) describes it as a substitute for more rigorous frequency analysis. Jenkins (1961) considers that the Schuster periodgram does not provide a very good estimate of spectral density at each wavelength and mentions that it produces a highly spiked spectrum even when white noise or random number sequences are analysed. Broom (1979) states that it is a general deficiency of the periodogram that each point represents a discrete, precisely defined wavelength whereas the points on a spectrogram with an appropriate filter, represent a range of wavelengths so that all cycles contribute to the plot and the spectrum is displayed in a clearer way (Jenkins and Watts, 1968; Williamson, 1975). The greatest advantage of the spectrogram is that statistical tests can readily be carried out on all points including the dominant peaks, but such tests are difficult to use on a Schuster periodogram (Broom, 1979). The spectrogram therefore provides a means of producing an estimate which eliminates noise, and provides a good estimate of cycles present in the raw data. It also allows statistical significance of peaks to be tested easily. For these reasons, the type

5) spectral analysis was felt to be the best technique available and was used in this study.

Autocorrelation and Fourier analysis using Tukey's lag window were employed to produce smoothed spectral estimates of each set of time series data. This was carried out for each of the individual recording channels as well as for channel Ø, the overall activity channel. The smoothed estimate was calculated as follows:-

$$\bar{R}(f) = 2\Delta\left(1+2\sum_{K=1}^{L-1} r_k W_k \cos 2\pi f K\Delta\right) \qquad 0 \leqslant f \leqslant \tfrac{1}{2}\Delta$$

Where R(f) is the spectral density

L is the truncation point

W_k is the lag window

k is the lag

$r_k = \frac{C_k}{C_0}$ (autocovariance function / autocorrelation function)

For the Tukey lag window, $W_k = 0.5(1 + \cos\frac{k}{4})$

The confidence limits, about a spectral density of 1.0 are given by,

$$\frac{DF}{X^2_{DF}(1-(\frac{\alpha}{2}))} \quad , \quad \frac{DF}{X^2_{DF}\ (\frac{\alpha}{2})}$$

Values for X^2_{DF} are given by a table of X^2 distribution giving cumulative probabilities for confidence internals (Simpson, Roe and Lewontin, 1960). The number of degrees of freedom of a smoothed spectral estimate using the Tukey lag window is

$$DF = \frac{8}{3}\frac{N}{L}$$

Where N is the number of sampling intervals. The chance probability of a theoretical spectrum falling outside its confidence interval at a particular frequency is denoted by α and α for 80% confidence intervals,

$$\alpha = 1.0 - 0.8 = 0.2$$

If spectral density is plotted on a log scale then the confidence interval line at a density of 1.0 as determined above can be transferred to any point on the smoothed spectral density estimate. However, due to the smoothing procedure carried out in this analysis, it is not always possible to assign 90% or 95% confidence intervals, even to time series with very strong sine wave components and little noise. For this reason, 80% confidence limits are standardly employed (Campbell and Shipp, 1974) and are used in this study. Each smoothed spectral estimate was studied and 80% confidence limits transferred to each peak and trough in order to detect significant frequencies present in the original time series. In addition, the interpretation of results is further complicated by the bandwidth of the Tukey window. The bandwidth of the Tukey window is given by,

$$b = \frac{1.33}{L} \quad \text{(for normalised estimates)}$$

or $$b = \frac{1.33}{L} \times \text{sampling frequency (for non-normalised estimates)}$$

In this study, estimates were not normalised and a sampling frequency of twice per hour was employed, therefore,

$$b = \frac{1.33}{L} \times 2$$

Peaks in the smoothed spectral estimate not separated by at least this bandwidth can not be resolved and should be regarded as non-significant. In all plots in the results section however, only those peaks showing statistical significance and which may be resolved are depicted with confidence intervals. Table B.2 (Appendix B) shows the cycles which may be resolved under the conditions employed in these experiments. A full discussion of the techniques used in this analysis is given in Appendix B and the programs used in the computation of data are listed in Appendix C.

Examples of spectral analysis of cyclic behaviour using this technique are given by Campbell and Shipp (1974) and Williamson (1975).

3-2.9 VERIFICATION OF ANALYTICAL TECHNIQUES

To ensure that the computer programs used in data manipulation were carrying out their intended function, time series data with known parameters were produced and the model subjected to the analysis described above.

Figures 3.4-3.7 show the smoothed spectral estimates of 4 pure sine waveforms with frequencies corresponding to 24, 12, 6 and 3 hours respectively. Figure 3.8 shows the smoothed spectral estimate of a time series with all four sine waves combined. All four peaks are again clearly defined. The procedure is therefore capable of detecting pure sine waveforms, but is it capable of detecting sine waveforms which are obscured by random components?

To obtain the periodicity of significant peaks on all plots in this section, find the reciprocal of the value for cycles/hour.

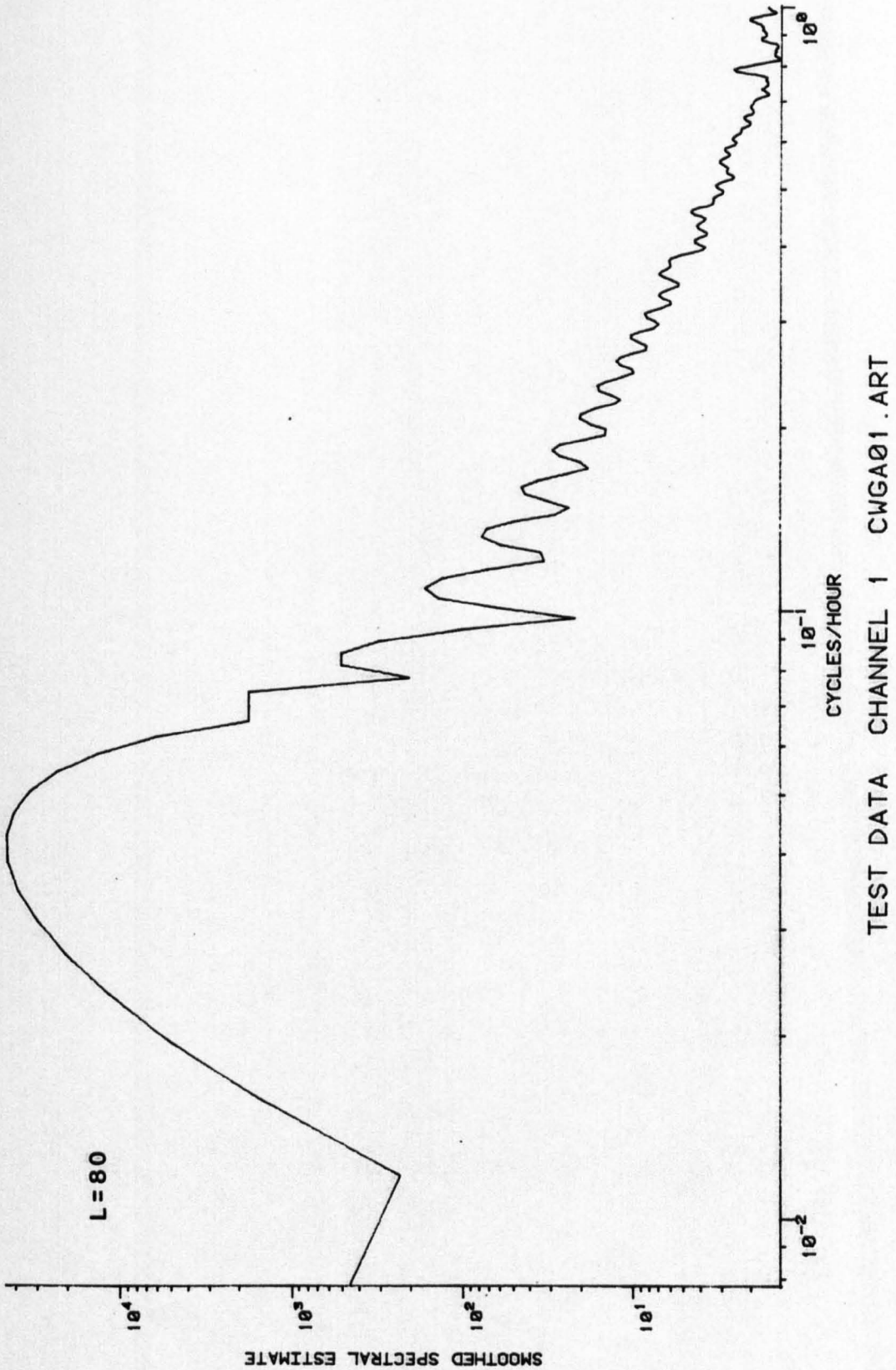


Figure 3.4
Smoothed spectral estimate of a sine wave with a periodicity of 24 hours.

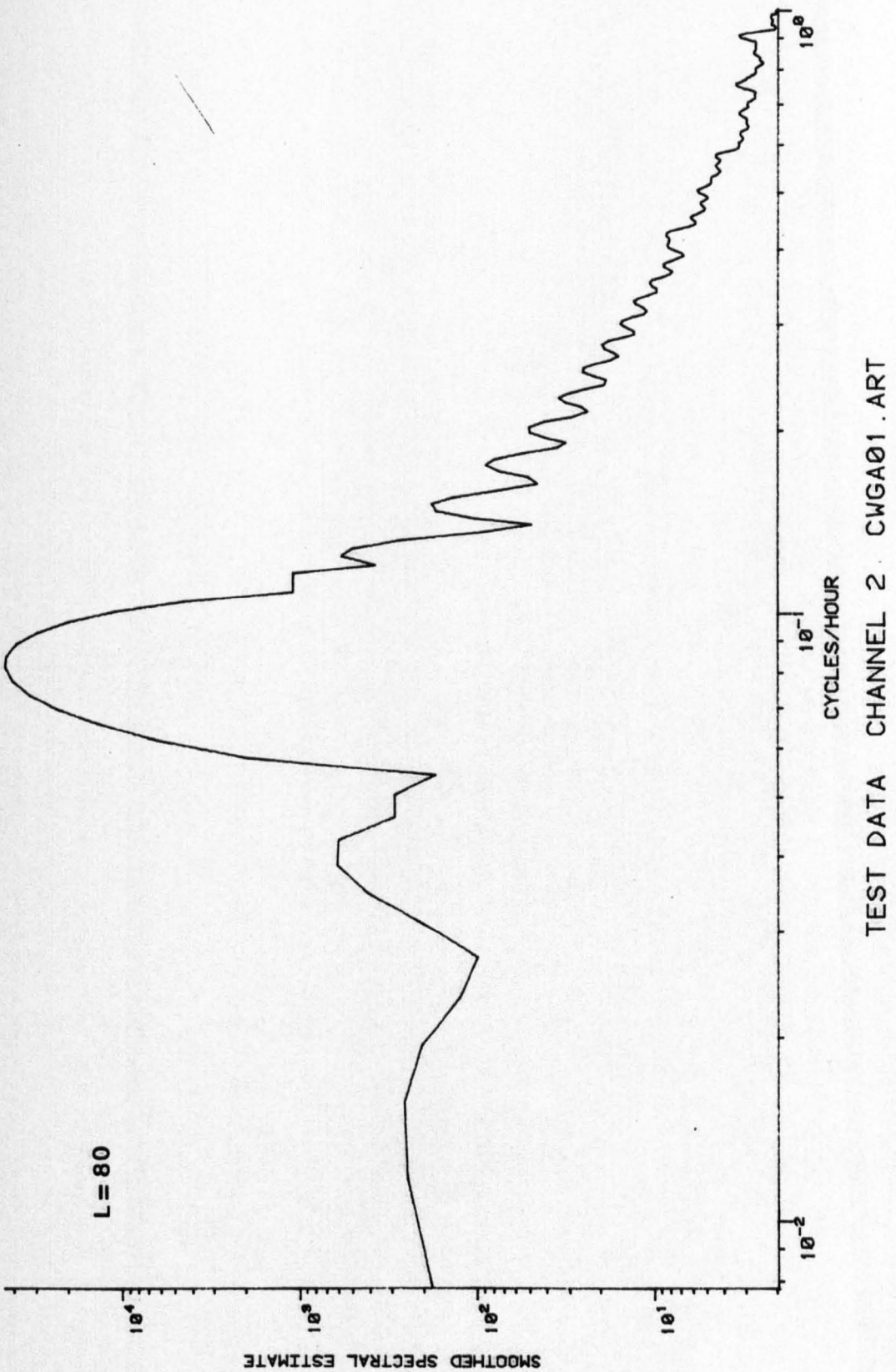


Figure 3.5
Smoothed spectral estimate of a sine wave with a periodocity of 12 hours.

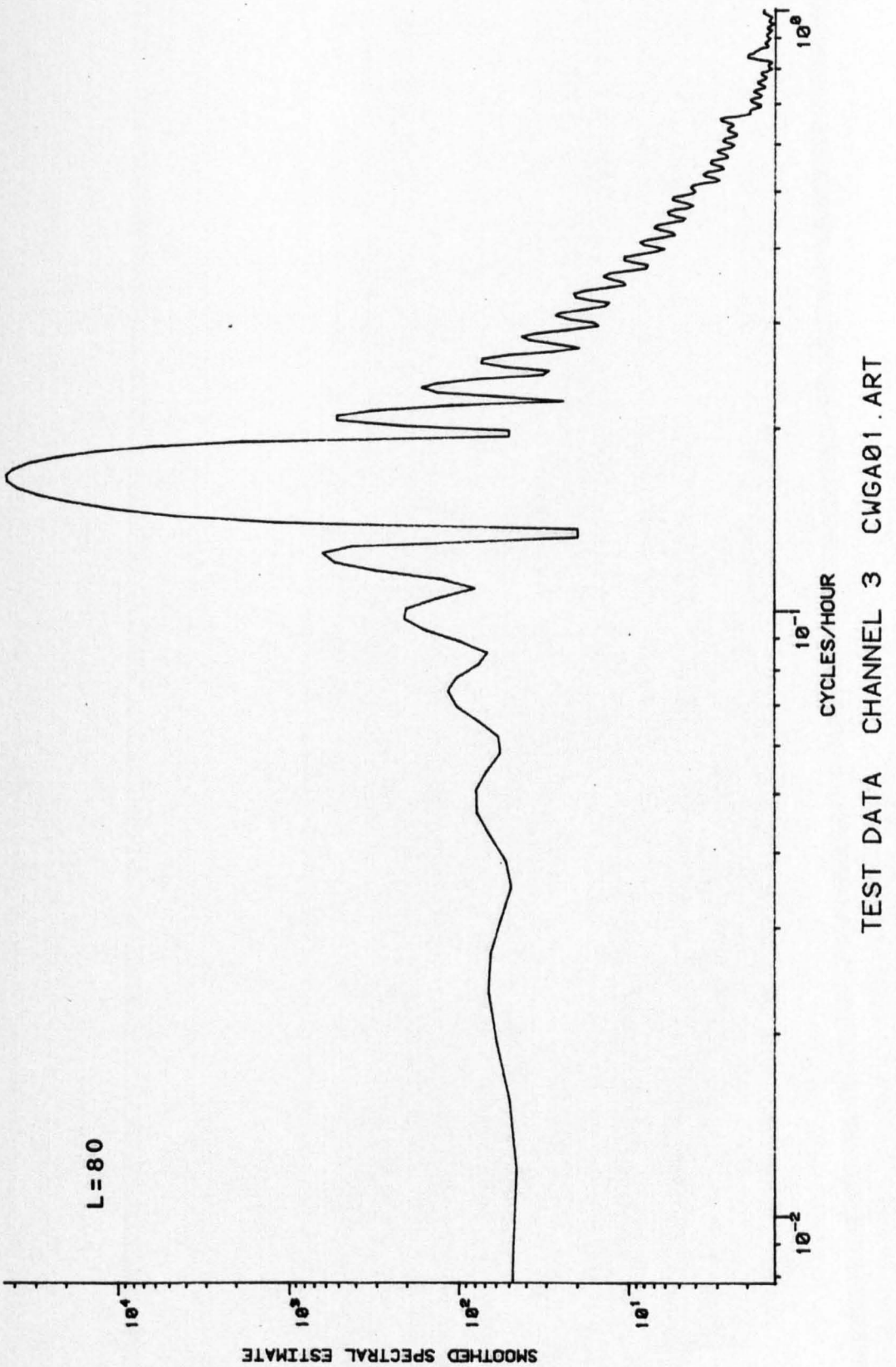


Figure 3.6
Smoothed spectral estimate of a sine wave with a periodicity of 6 hours.

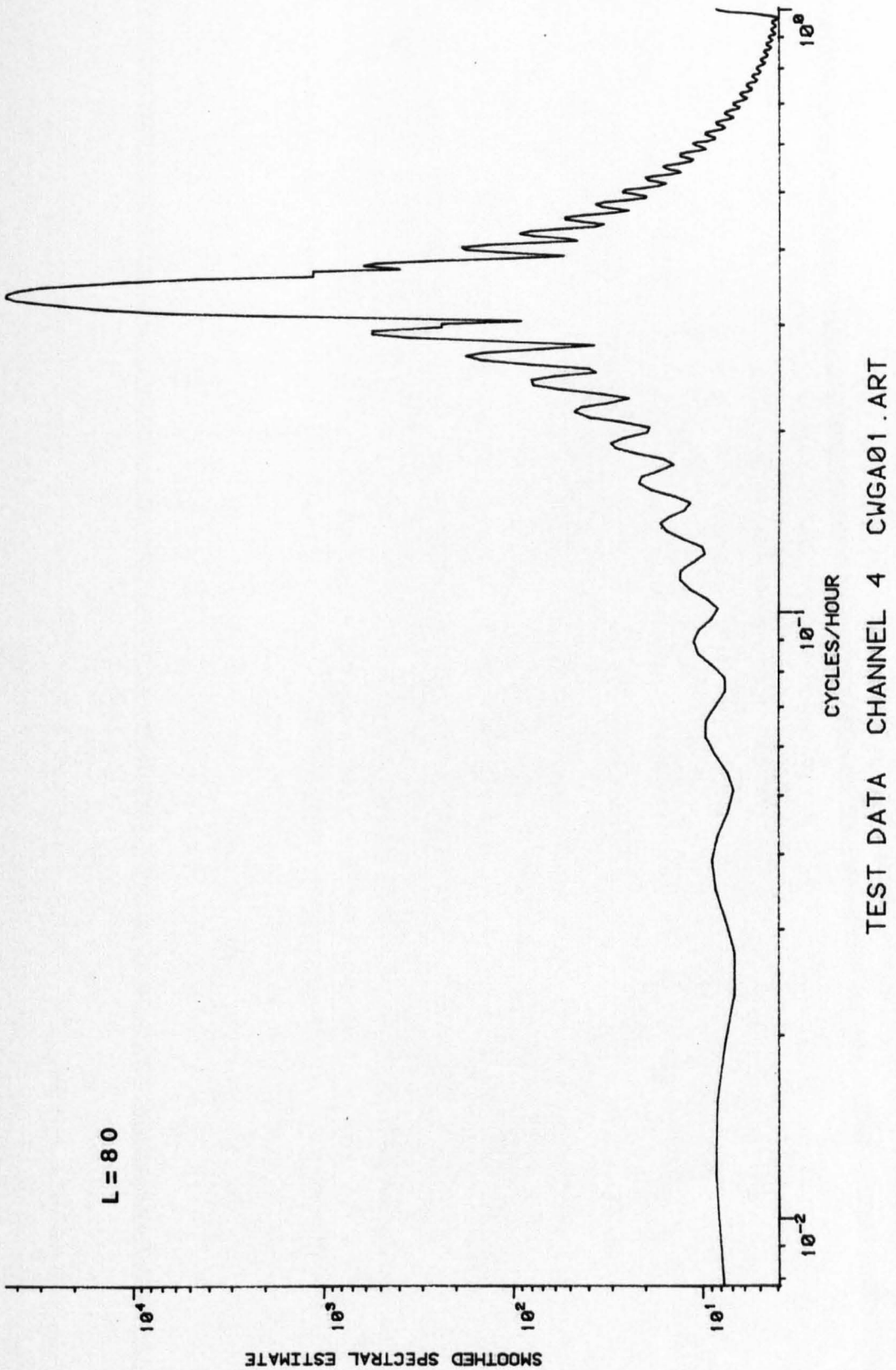


Figure 3.7
Smoothed spectral estimate of sine wave with a periodicity of 3 hours.

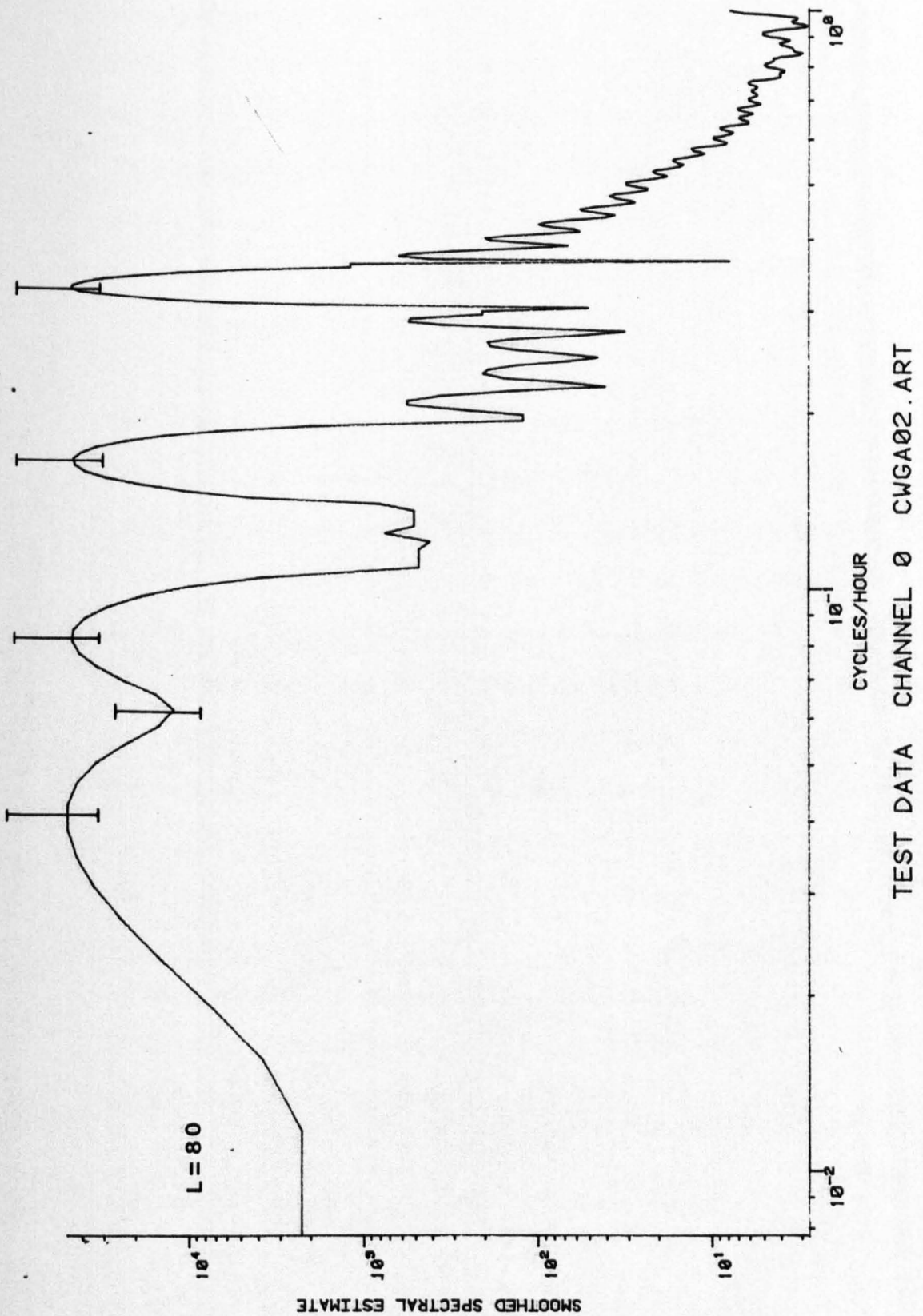


Figure 3.8
Smoothed spectral estimate of a time series with the periodicities shown in Figures 3.4-3.7 combined.

Figure 3.9 shows the autocorrelation function of a sample of random noise, produced by a random number generator. Figure 3.10 shows the same sample of random noise with four sine waves of known frequency superimposed. Each sine wave has an amplitude of 50 units while the noise component has an amplitude of 200 units. It is obvious at this stage that the data in Figure 3.10 shows some periodicity. However, the frequency or frequencies of the periodicity is not immediately obvious.

The unsmoothed spectral estimate or Fourier transform of these data (Figure 3.11) shows four major peaks corresponding to cycles of 24 hours, 12 hours, 6 hours and 3 hours. It is not an easy task however, to determine whether these peaks are significant. In addition, it is possible that some of the smaller peaks may represent periodicities present in the raw data. The smoothed spectral estimate (Figure 3.12), on the other hand, allows confidence limits to be calculated for each of the peaks. In this example, the four peaks of 24, 12, 6 and 3 hour cycles correspond with the known periodicities present in the raw data. A similar sample in which the noise component is eight times the amplitude of the four sine waves is shown in Figure 3.13. At least three of the major peaks are still visible. The confidence limits indicate that these peaks are not significant; however, they do indicate the frequencies known to exist in the sample.

The computer programs and the analytical technique therefore carry out their intended function and have been shown to be capable of detecting periodicities obscured by high levels of noise.

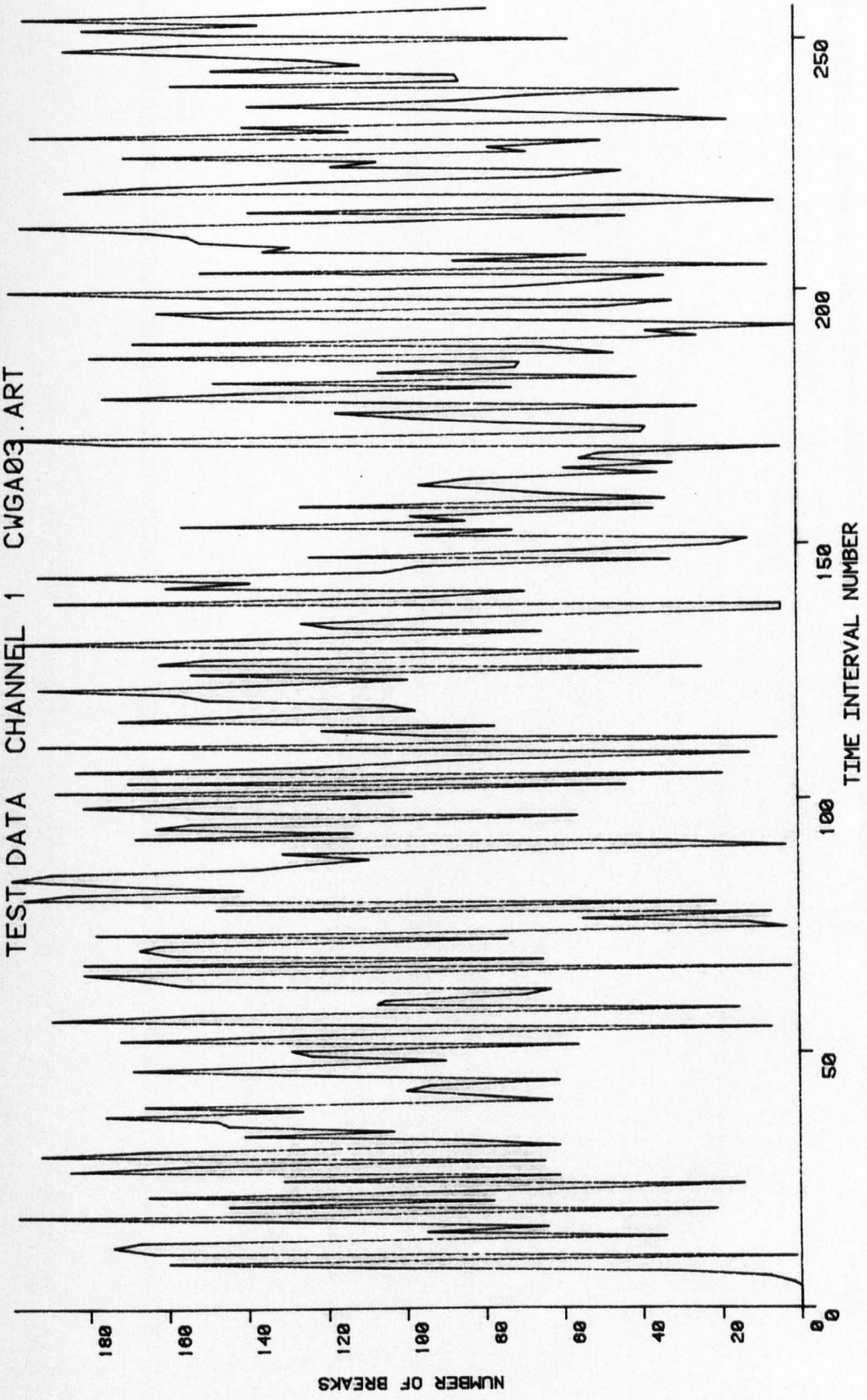


Figure 3.9
Sample of random data produced by a random number generator.

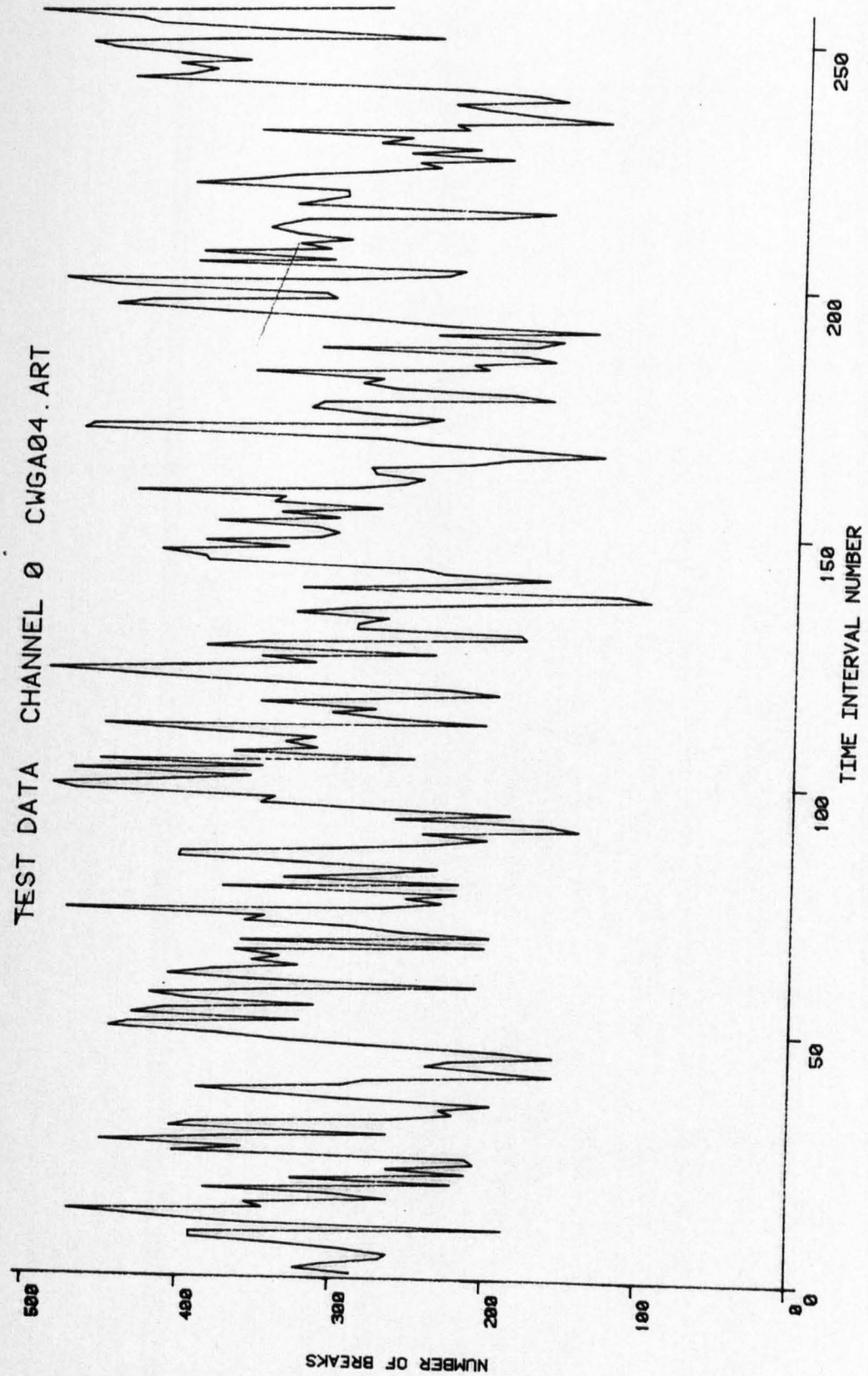


Figure 3.10
Sample of random data with 4 sine waves of known frequency superimposed.

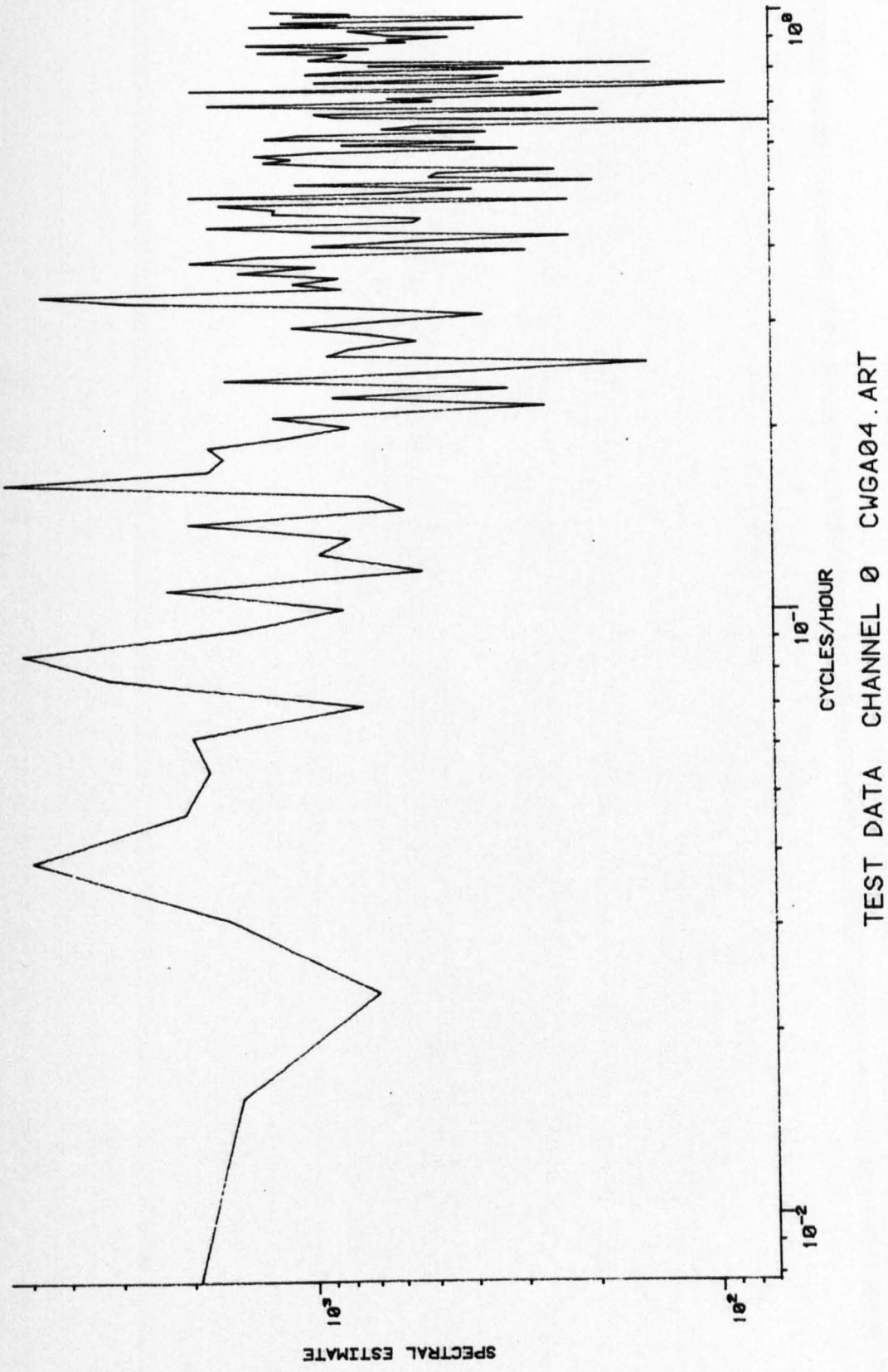


Figure 3.11
Fourier transform or unsmoothed spectral estimate of the time series shown in Figure 3.10.

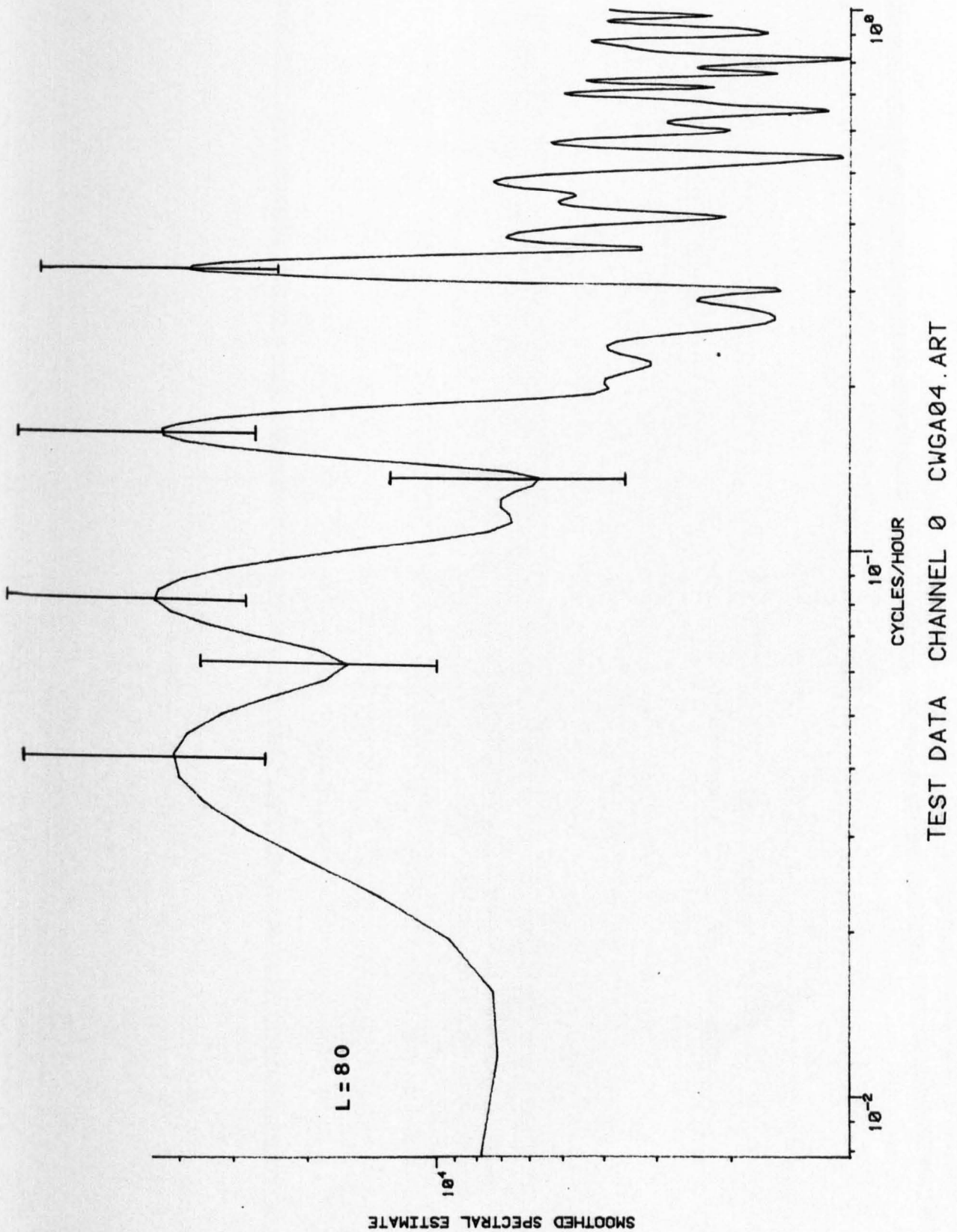


Figure 3.12
Smoothed spectral estimate of the time series shown in Figure 3.10. The four peaks depicted with error bars correspond with the sine waves known to exist in the time series.

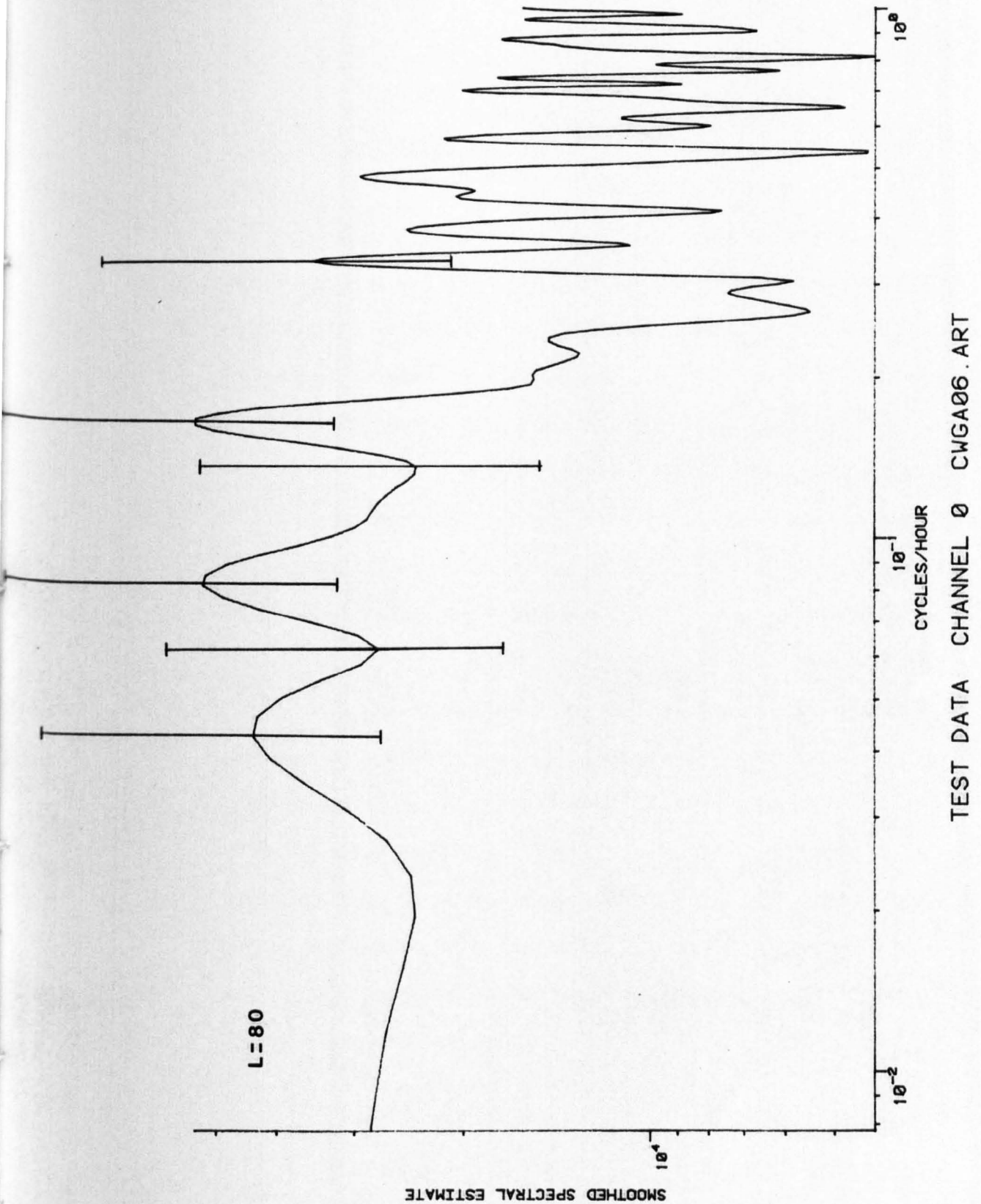


Figure 3.13
Smoothed spectral estimate of a time series similar to that shown in Figure 3.10, where the noise component is eight times the amplitude of the four sine waves.

3-3 RESULTS

3-3.1 ACCLIMATISATION

The locomotor activity of eight individual crabs during their 24 hour acclimatisation periods are shown in Figures 3.14-3.21. Table 3.0 describes the symbols employed on subsequent plots. The subsequent locomotor activity shown by each of the crabs during the experimental period is shown in Figures 3.22-3.29. Table 3.1 summarises the range of activity (number of light beam breaks per 30 minute time interval) displayed by each of the crabs during the acclimatisation and experimental periods. Five of the eight crabs (D13, D14, TØ7, TD8, T13) show peaks of activity during the acclimatisation period which are larger than peak activity shown during the experimental period. In each case, these peaks of activity occur within the first eight hour period of acclimatisation. The three other crabs (TØ6, TD9, T11) show no hyperactivity during the acclimatisation period, the levels of activity in each case falling within the range of activity displayed over the five day experimental period. In all cases, locomotor activity shown in the final 16 hours of acclimatisation is of a similar range to locomotor activity displayed during experimental recording.

For explanation of symbols used on all Figures in this section see Table 3.0 (page 167).

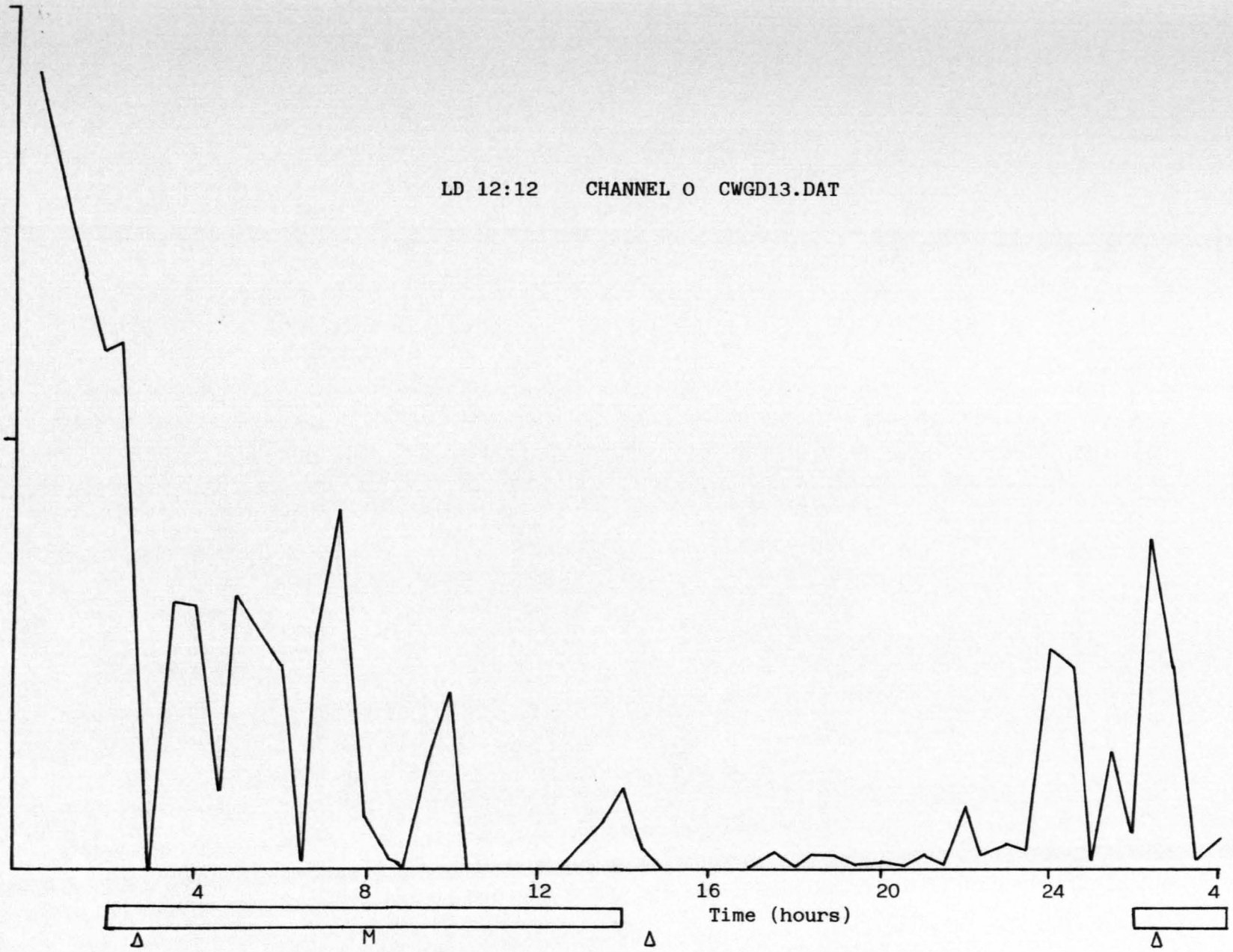


Figure 3.14
Activity shown by crab D13 during acclimatisation period and first four hours of experimental period.

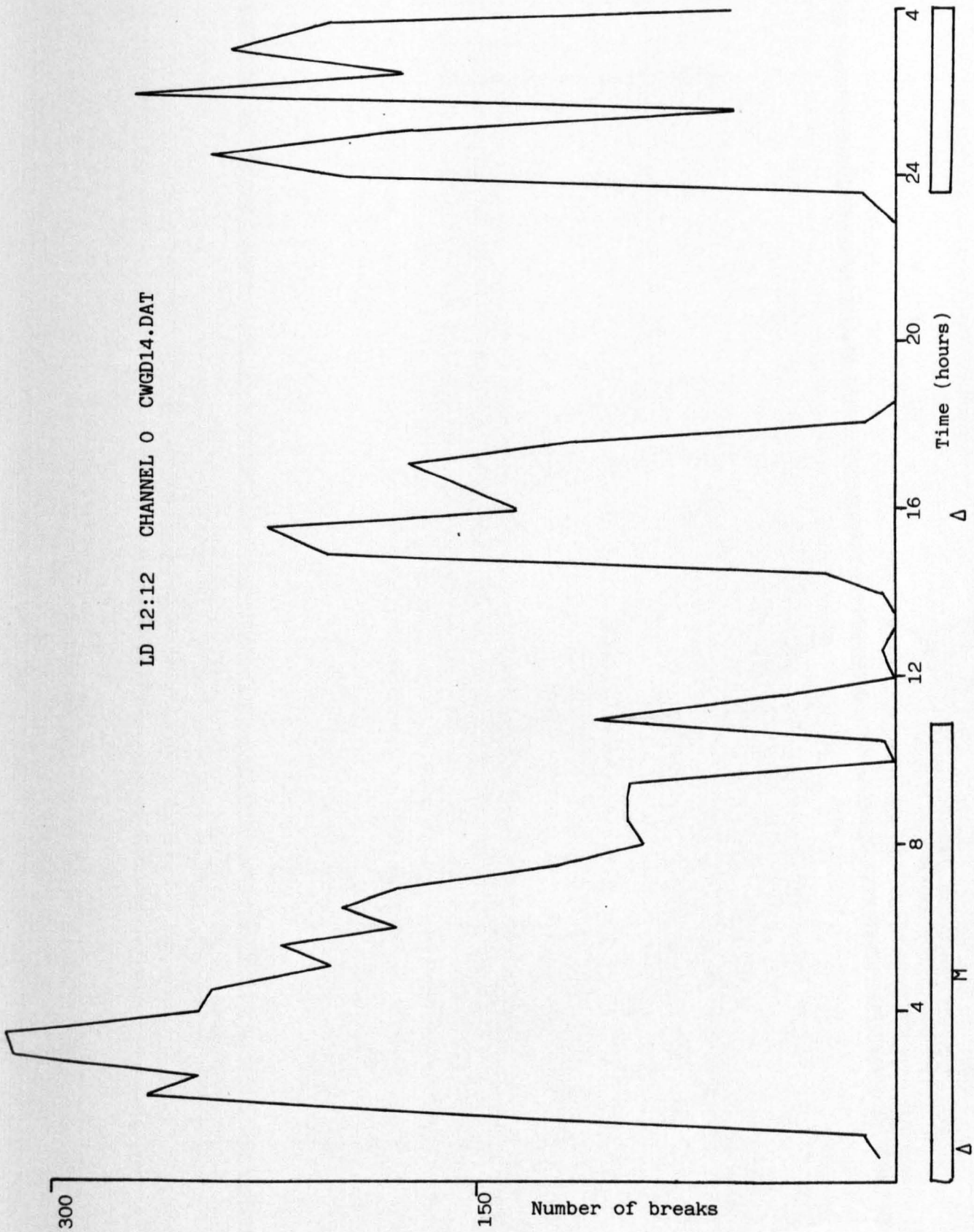


Figure 3.15
Activity shown by crab D14 during acclimatisation period and first four hours of experimental period.

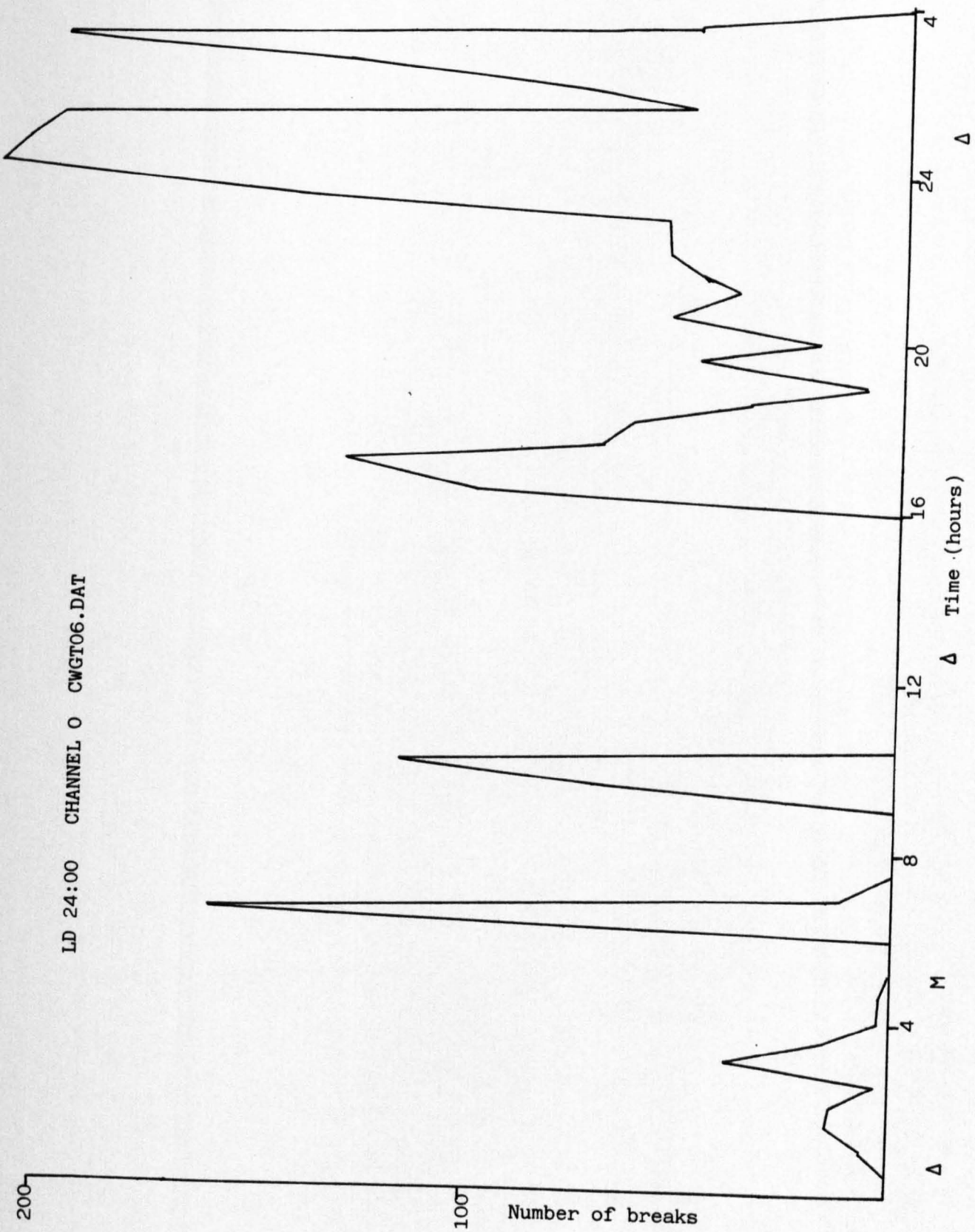


Figure 3.16
Activity shown by crab T06 during acclimatisation period and first four hours of experimental period.

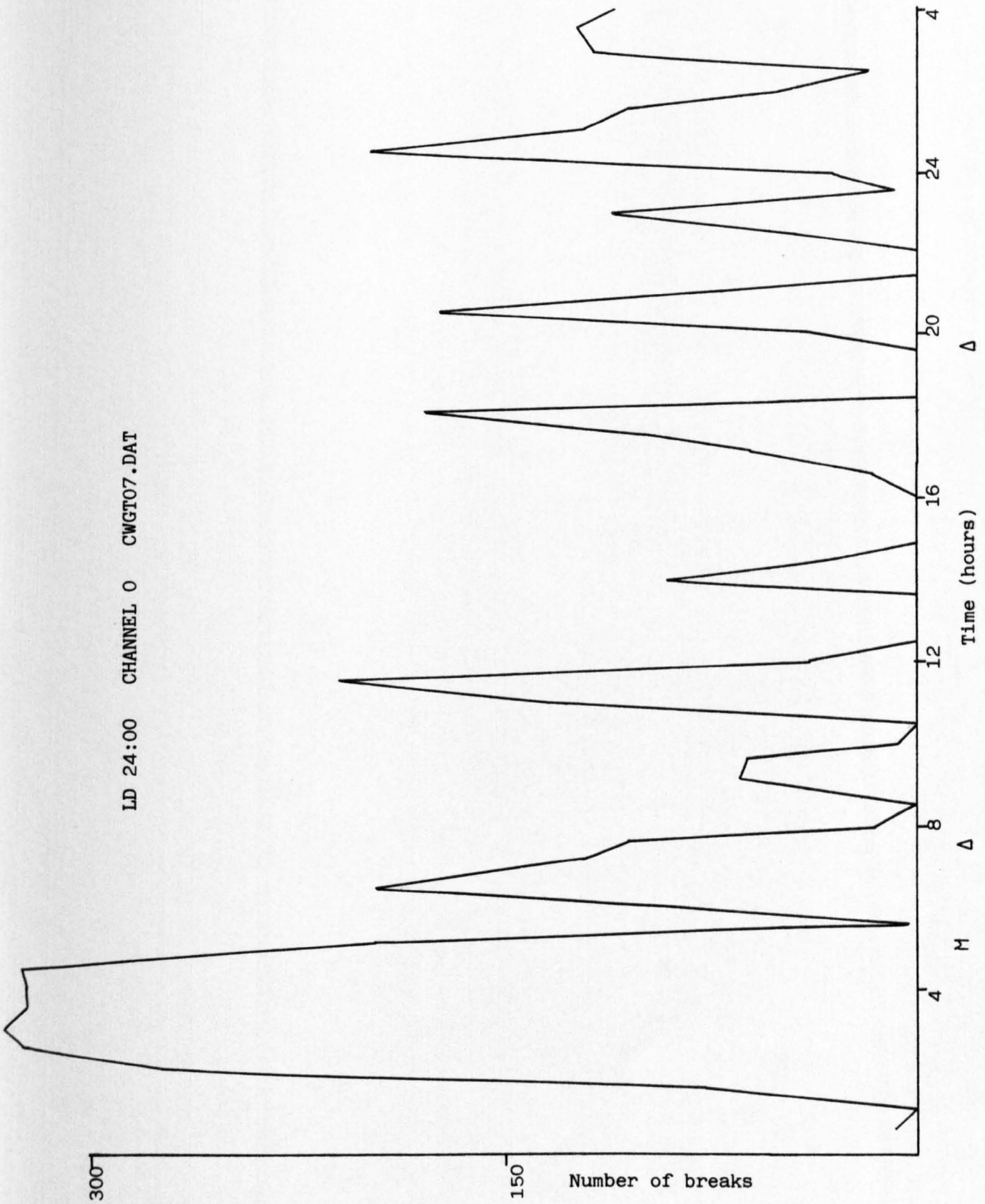


Figure 3.17
Activity shown by crab T07 during acclimatisation period and first four hours of experimental period.

Figure 3.18
Activity shown by crab TD8 during acclimatisation period and first four hours of experimental period.

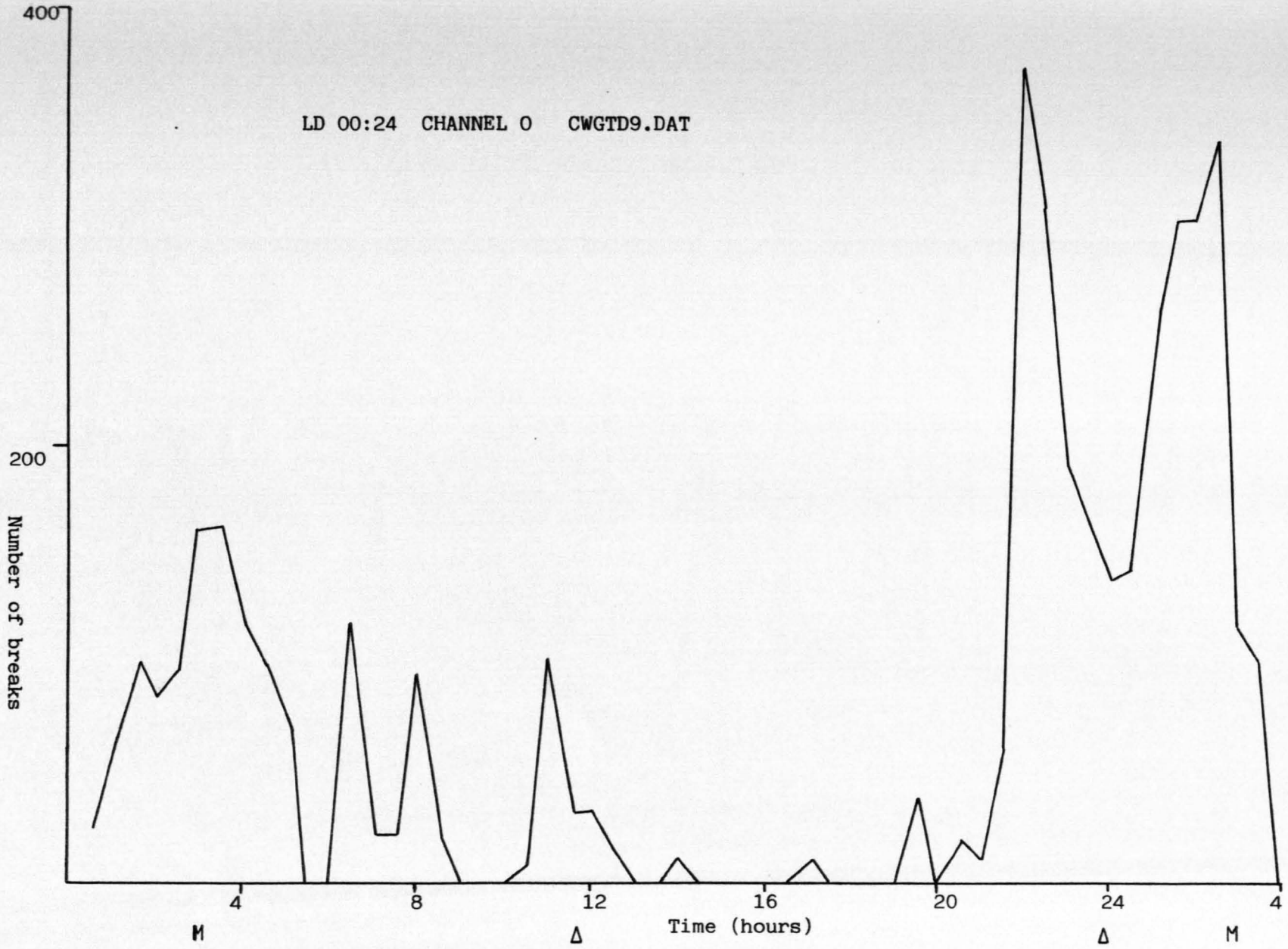


Figure 3.19
Activity shown by crab TD9 during acclimatisation period and first four hours of experimental period.

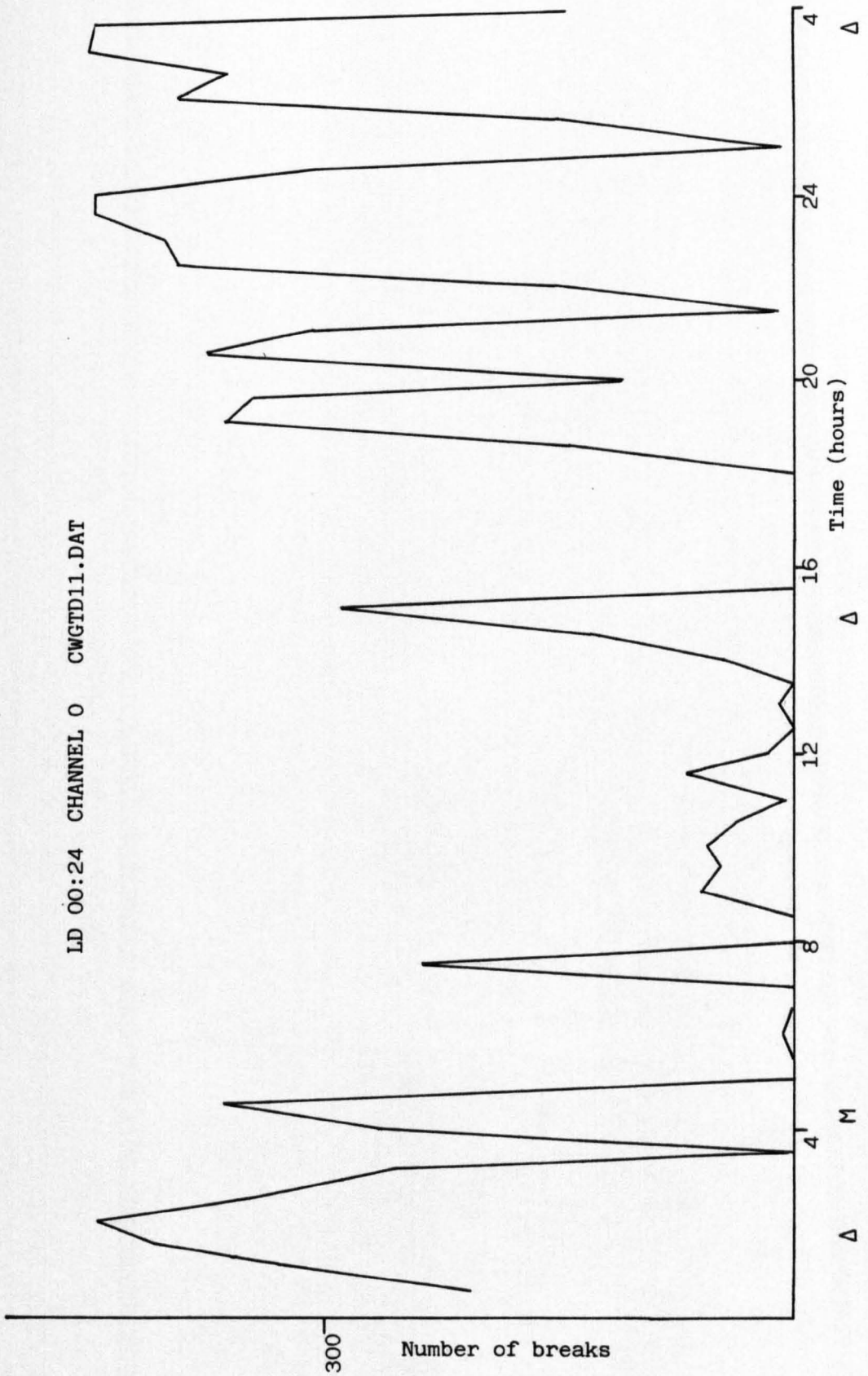


Figure 3.20
Activity shown by crab TD11 during acclimatisation period and first four hours of experimental period.

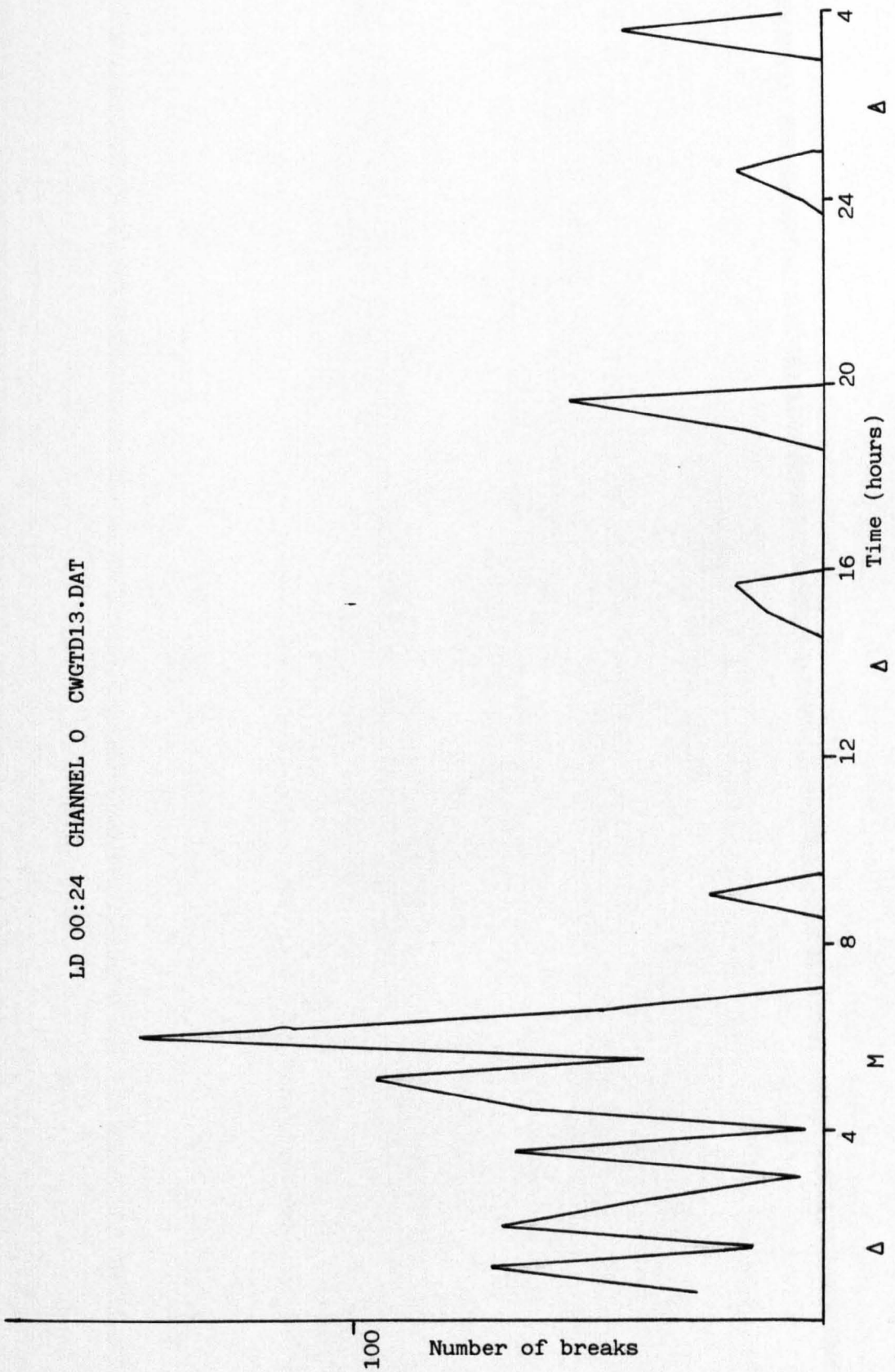
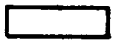


Figure 3.21
Activity shown by crab TD13 during acclimatisation period and first four hours of experimental period.

Table 3.0

Key to symbols employed on diagrams in this section.

SYMBOL	DEFINITION
L	Truncation point (see Appendix B)
M	Mid-night
△	Occurrence of high tide at collection site
	Dark phase of light cycle

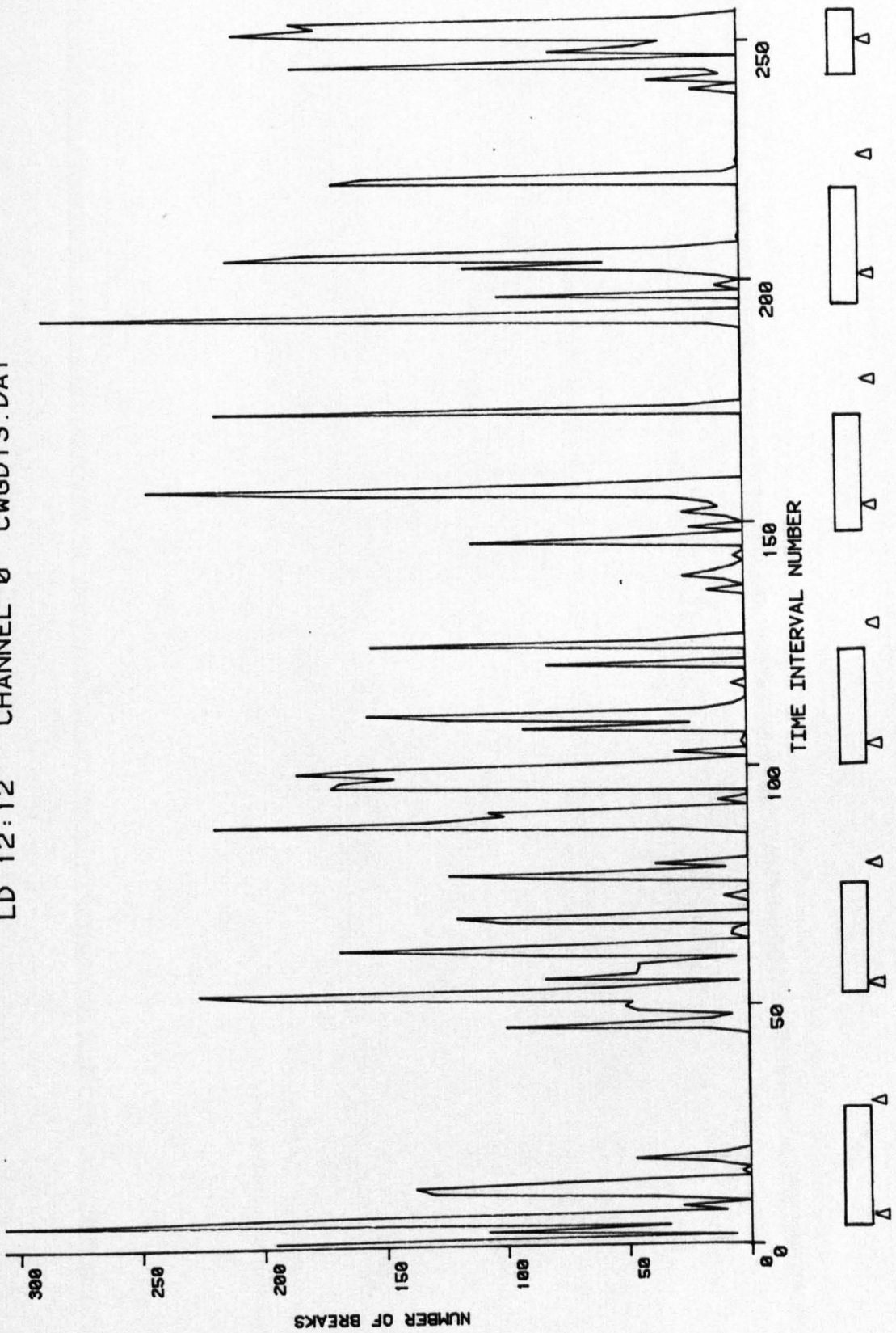


Figure 3.22
Plot of activity against time for crab D13.

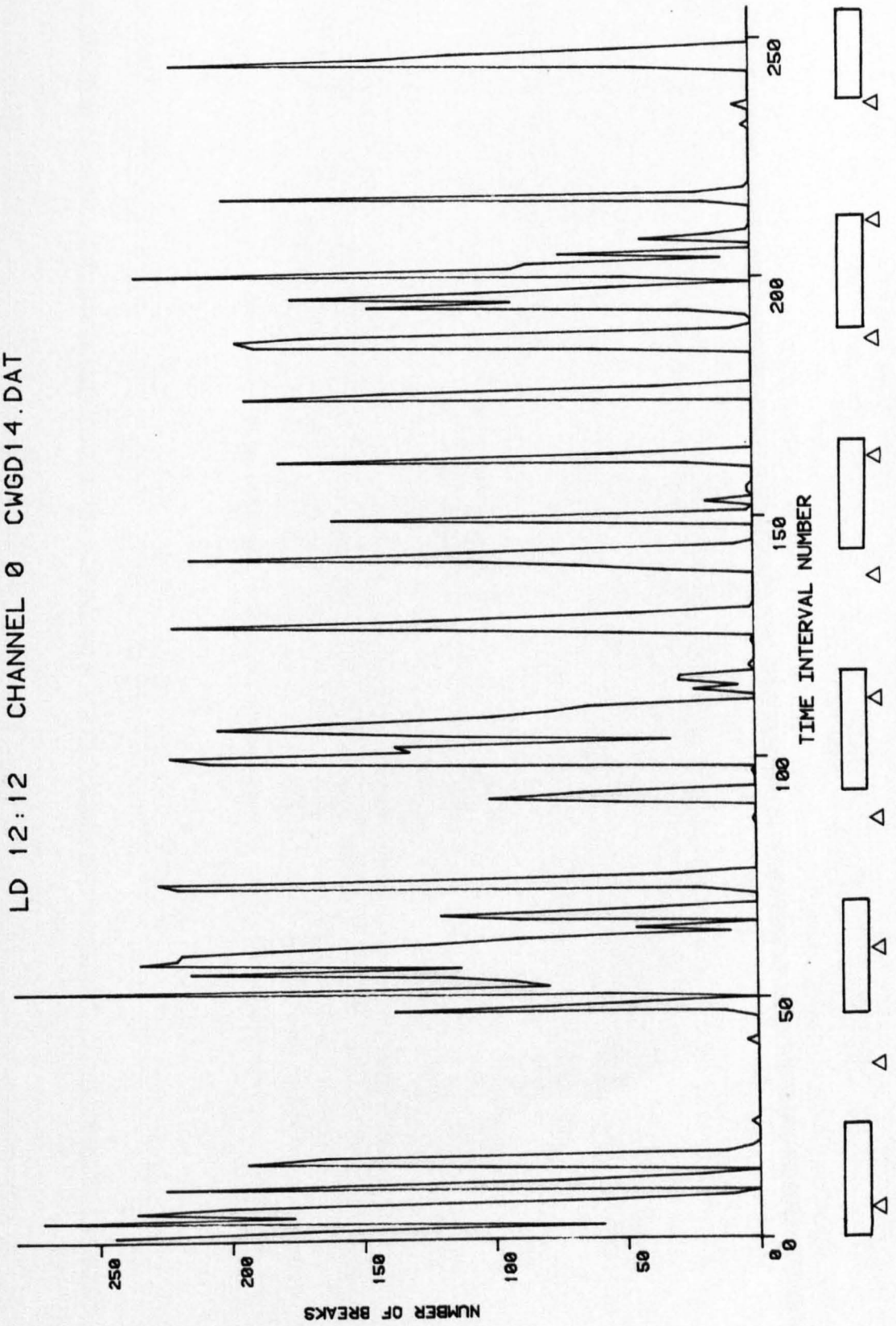


Figure 3.23
Plot of activity against time for crab D14.

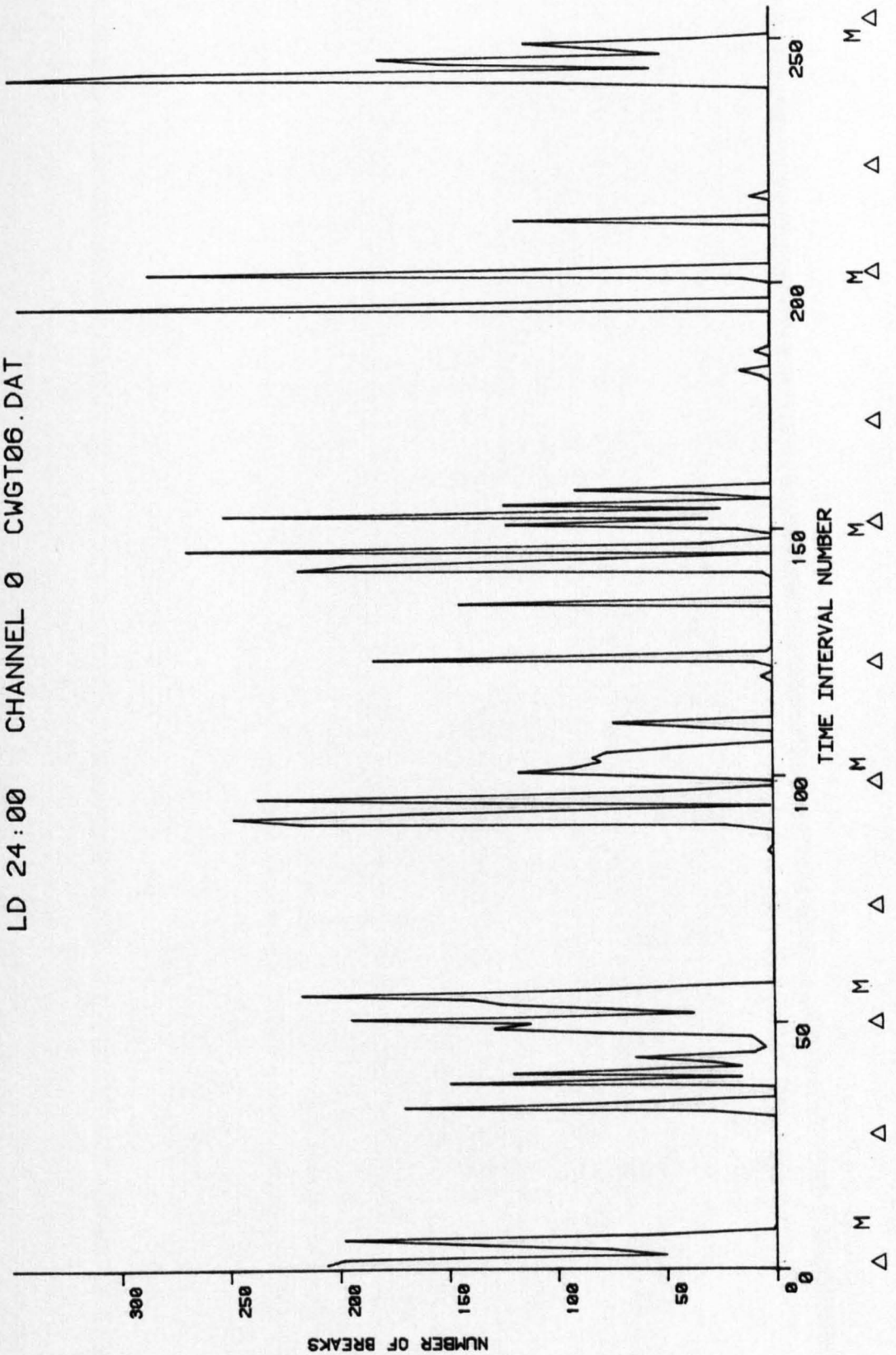


Figure 3.24
Plot of activity against time for crab T06.

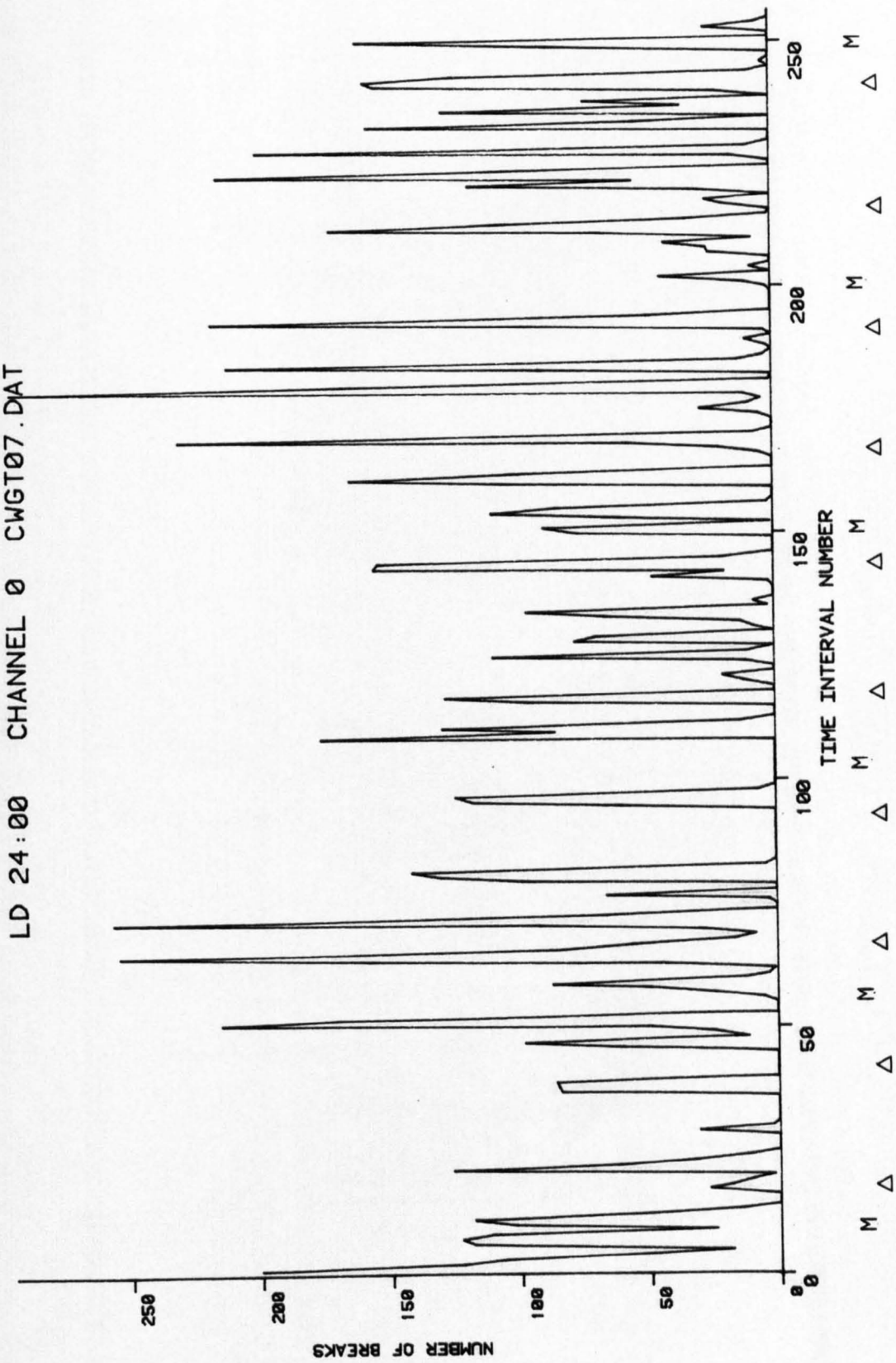


Figure 3.25
Plot of activity against time for crab T07.

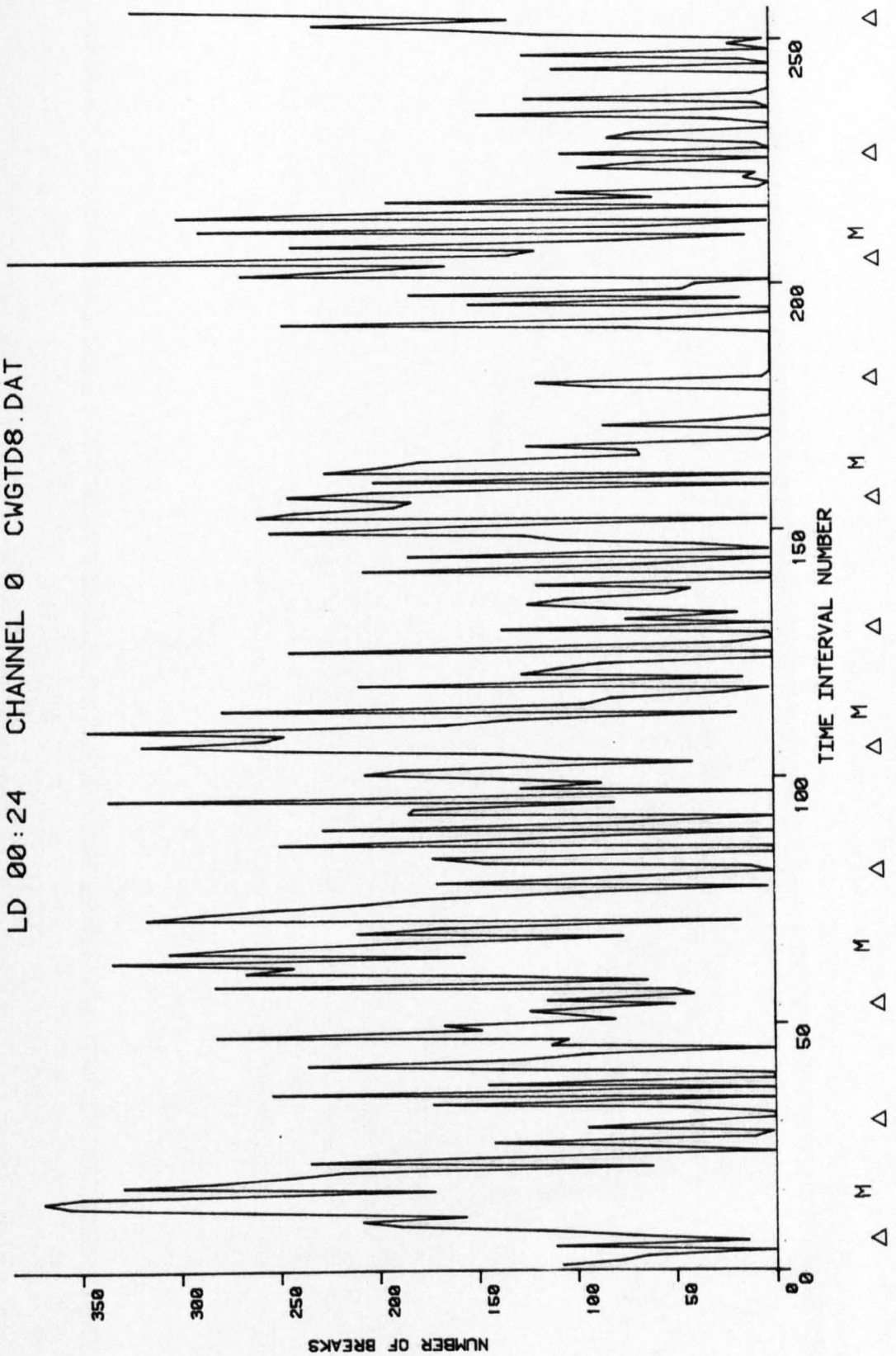


Figure 3.26
Plot of activity against time for crab TD8.

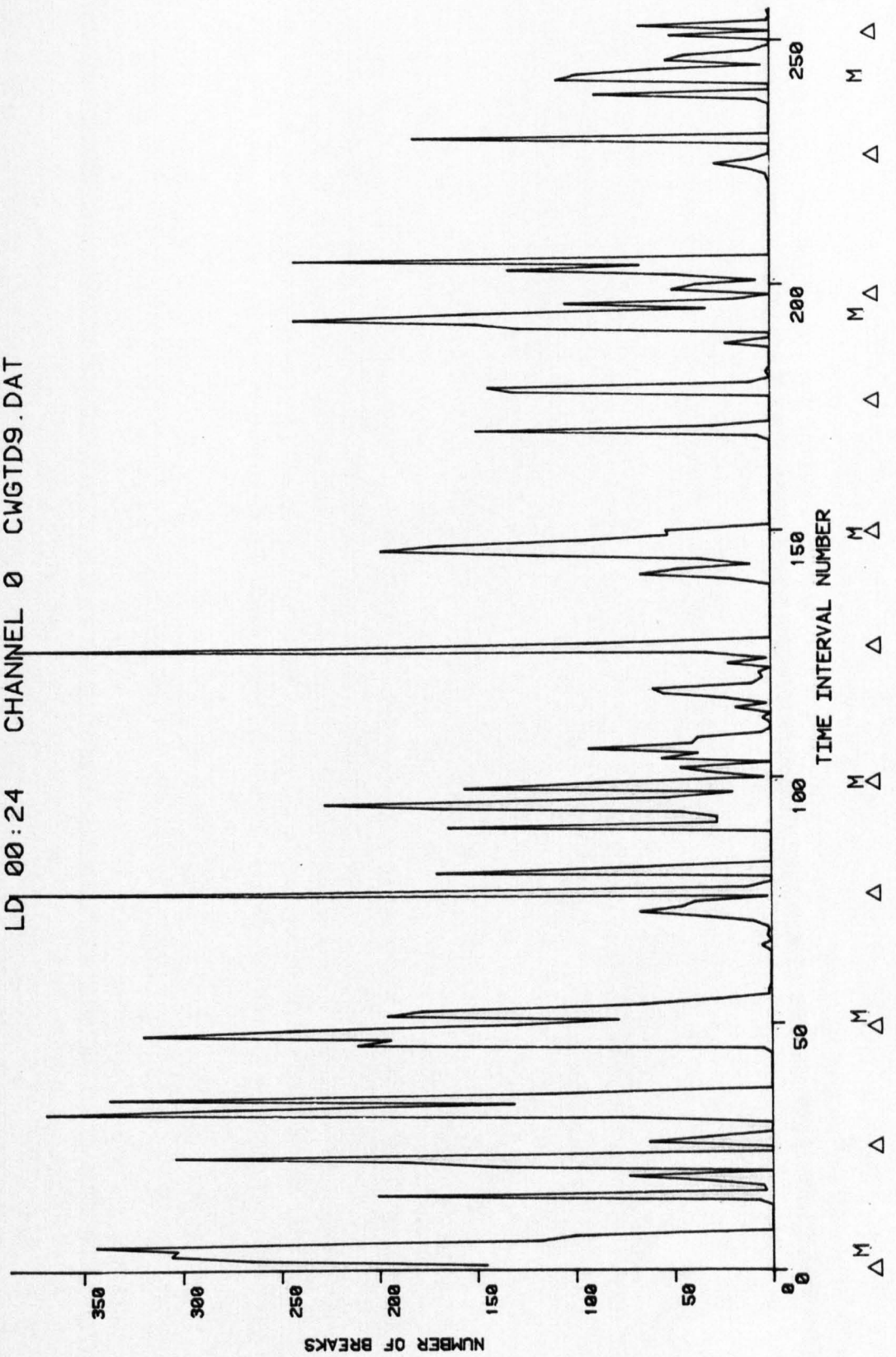


Figure 3.27
Plot of activity against time for crab TD9.

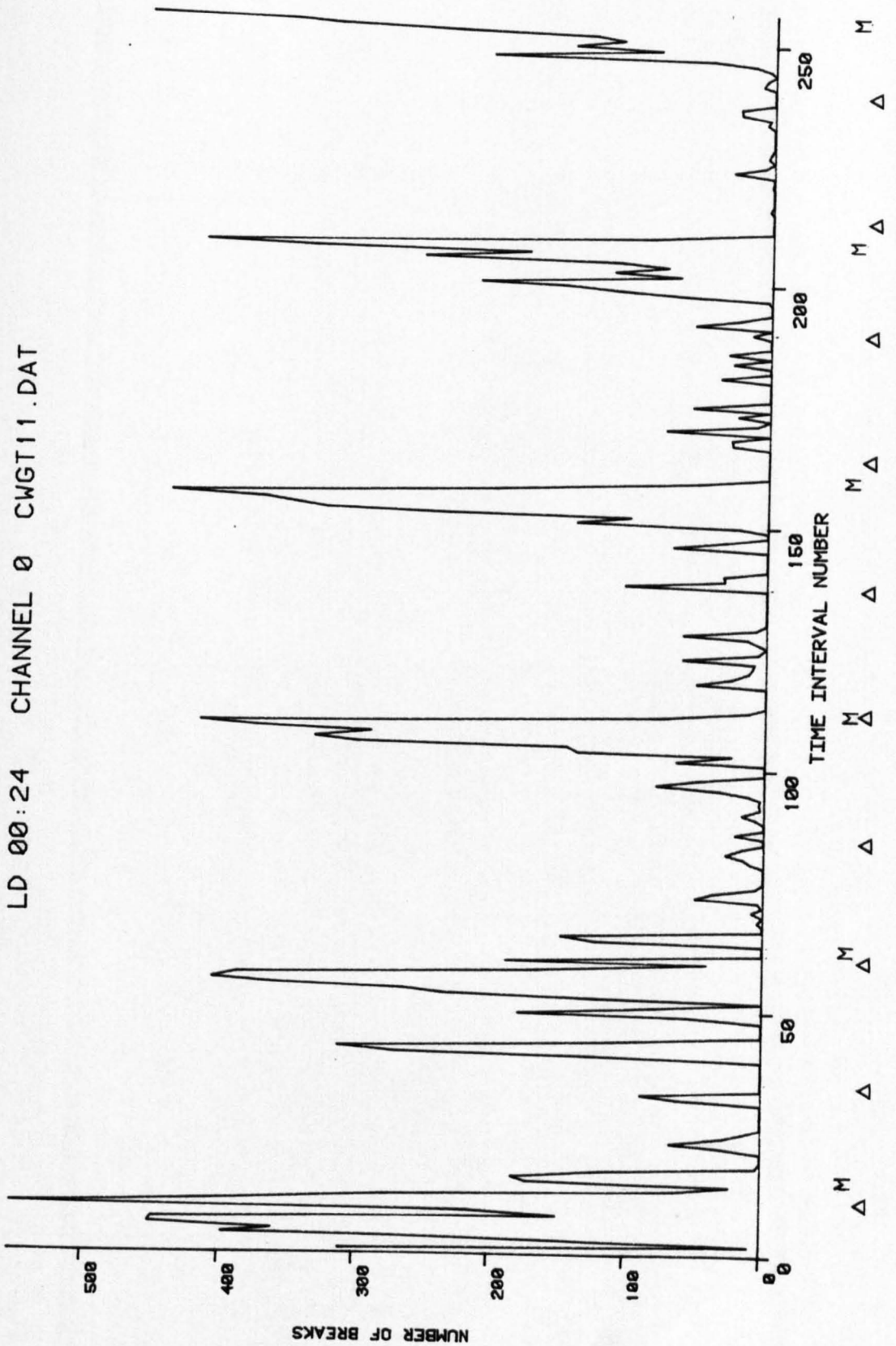


Figure 3.28
Plot of activity against time for crab TD11.

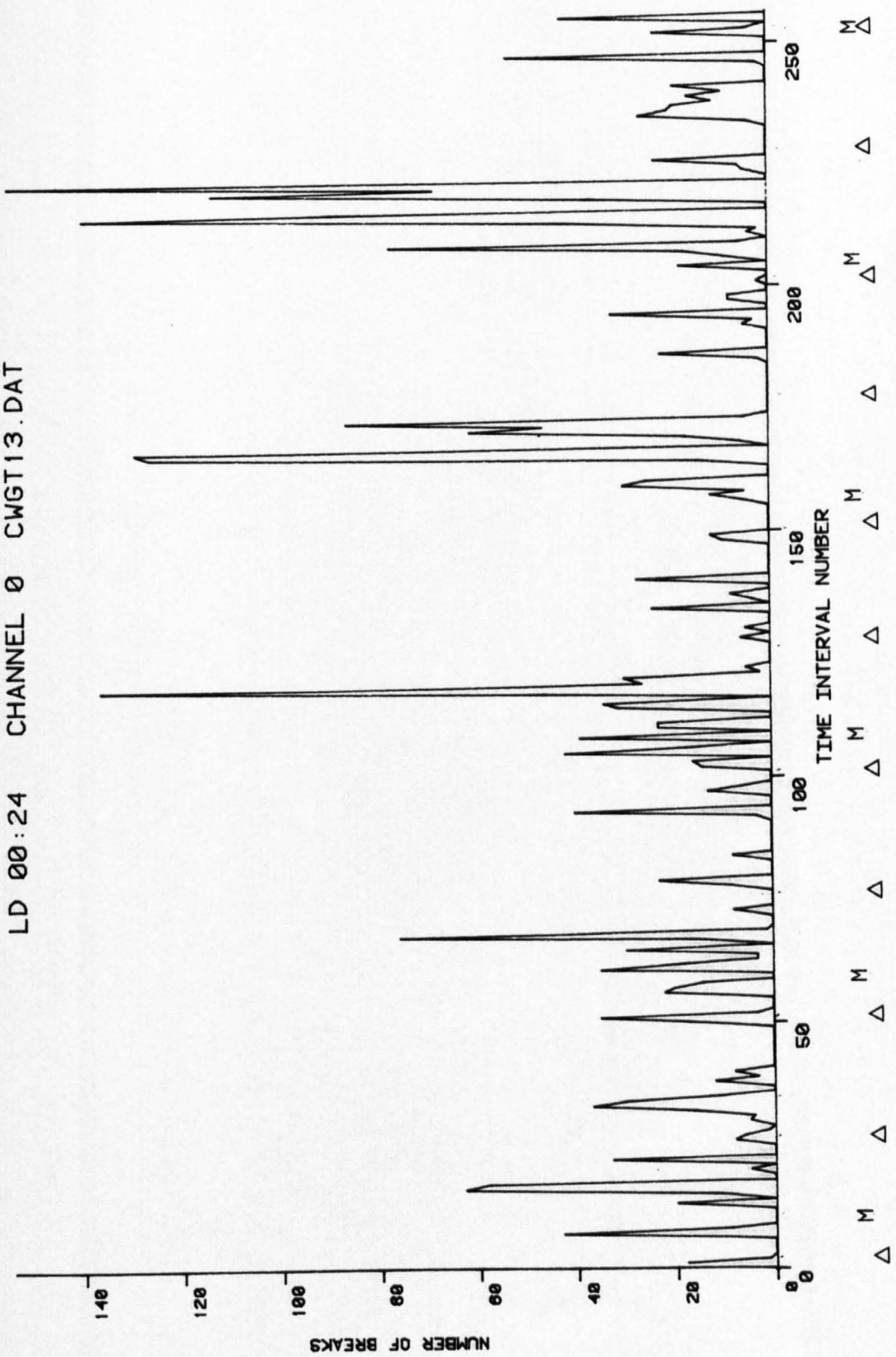


Figure 3.29
Plot of activity against time for crab TD13.

Table 3.1
Summary of the range of activity shown by each crab during acclimatisation and experimental periods.

Experimental Identification	Peak activity displayed during 2 hr periods in the first 8 hrs of acclimatisation.				Range of activity shown during final 16 hrs of acclimatisation.	Range of activity shown during experimental period.
	0-2	2-4	4-6	6-8		
D13	740	490	252	355	0-204	0-306
D14	267	317	243	199	0-226	0-281
T06	19	39	3	160	0-213	0-345
T07	275	332	326	198	0-212	0-294
TD8	396	248	246	219	0-178	0-384
TD9	100	161	102	122	0-375	0-387
TD11	444	348	362	119	0-451	0-553
TD13	71	79	159	48	0-54	0-154

In each case activity is measured as the number of light beam breaks in a 30 minute period.

3-3.2 3-DIMENSIONAL PLOTTING

Figures 3.30-3.33 show the four main locomotor patterns displayed by L. depurator in the laboratory. Figure 3.30 shows the activity pattern produced by crab DO3 (LD 12:12). Most of the activity in this case occurred around channel 1, the crab only moving across the tank occasionally. During only three separate bursts of activity did the crab move to the opposite end of the tank and break light beam number 6. The plot of overall activity against time for this experiment, however, gives no indication of the tendency of this crab to favour one side of the aquarium. Similarly, Figure 3.31 shows the activity pattern of a crab which favours the channel 1 end of the tank. However, in this case, the overall level of activity is very low, the crab remaining stationary for long periods. Bursts of activity, when they occurred were very short and involved very few light beam breaks.

The overall locomotor activity shown by experimental crab TD8 (LD 0:24) is given in Figure 3.26. This crab shows a very high level of locomotor activity throughout the 5 day experimental period. Figure 3.32 shows clearly however, that no particular area of the aquarium is favoured by this crab and activity occurs evenly throughout.

In each of the three cases mentioned above, significant rhythmic components may exist within the locomotor patterns. If they do exist, they are not immediately evident by visual examination of the activity patterns. The fourth major locomotor pattern however, shows a clear cyclic component. Figure 3.33 shows one such locomotor pattern. In this case, activity is not confined to any

Figure 3.30

3-dimensional plot of activity shown by crab DØ3 (LD 12:12). Activity is concentrated on channel 1 while activity only occurs on channel 6 on three separate occasions. Table 3.0 describes sybmols employed on all plots in this section.

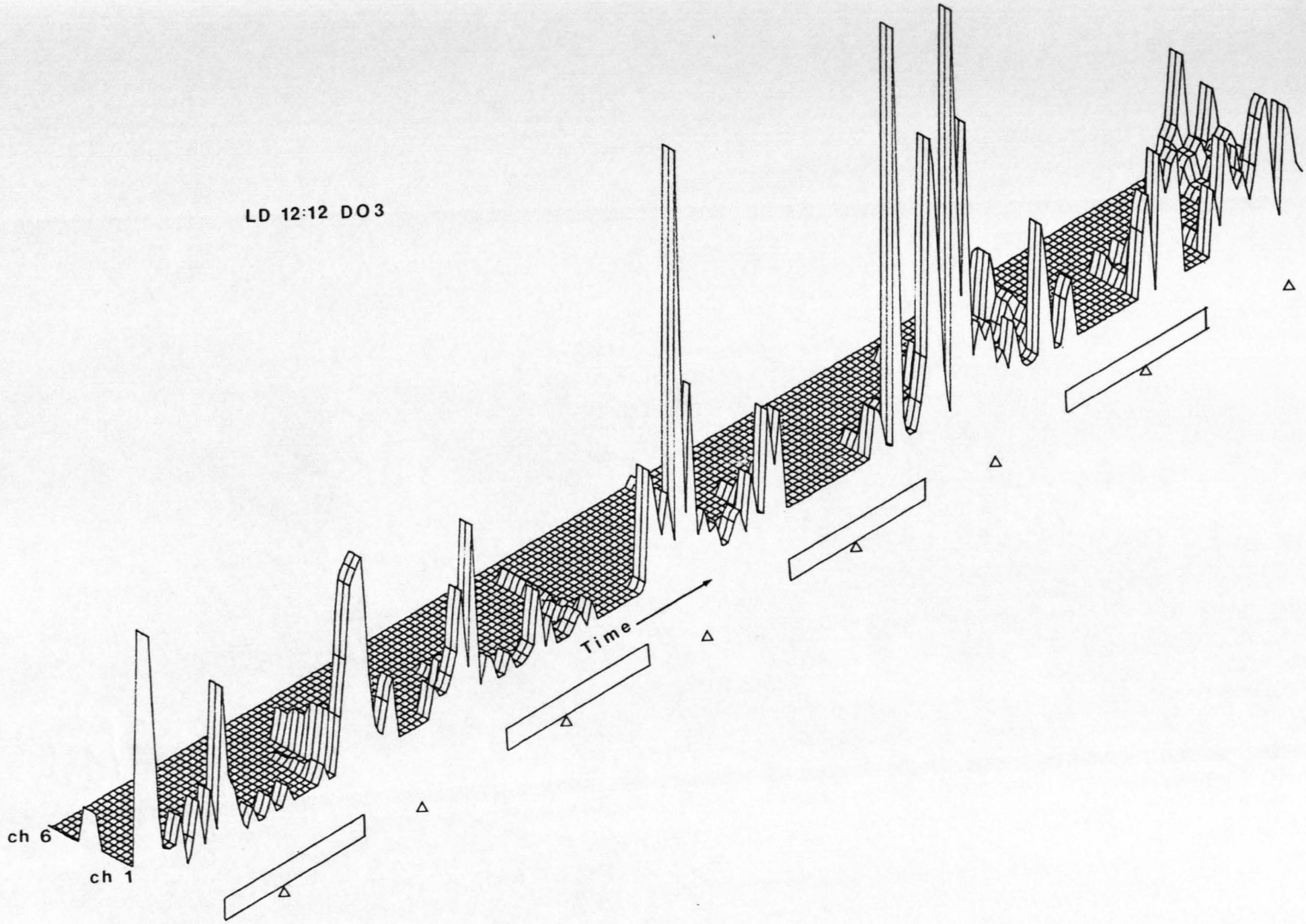

LD 12:12 DO3
Time
ch 6
ch 1

Figure 3.31

3-dimensional plot of activity pattern of crab DØ5 (LD 12:12) showing a very low overall level of activity. There is some concentration of activity at the channel 1 side of the experimental tank.

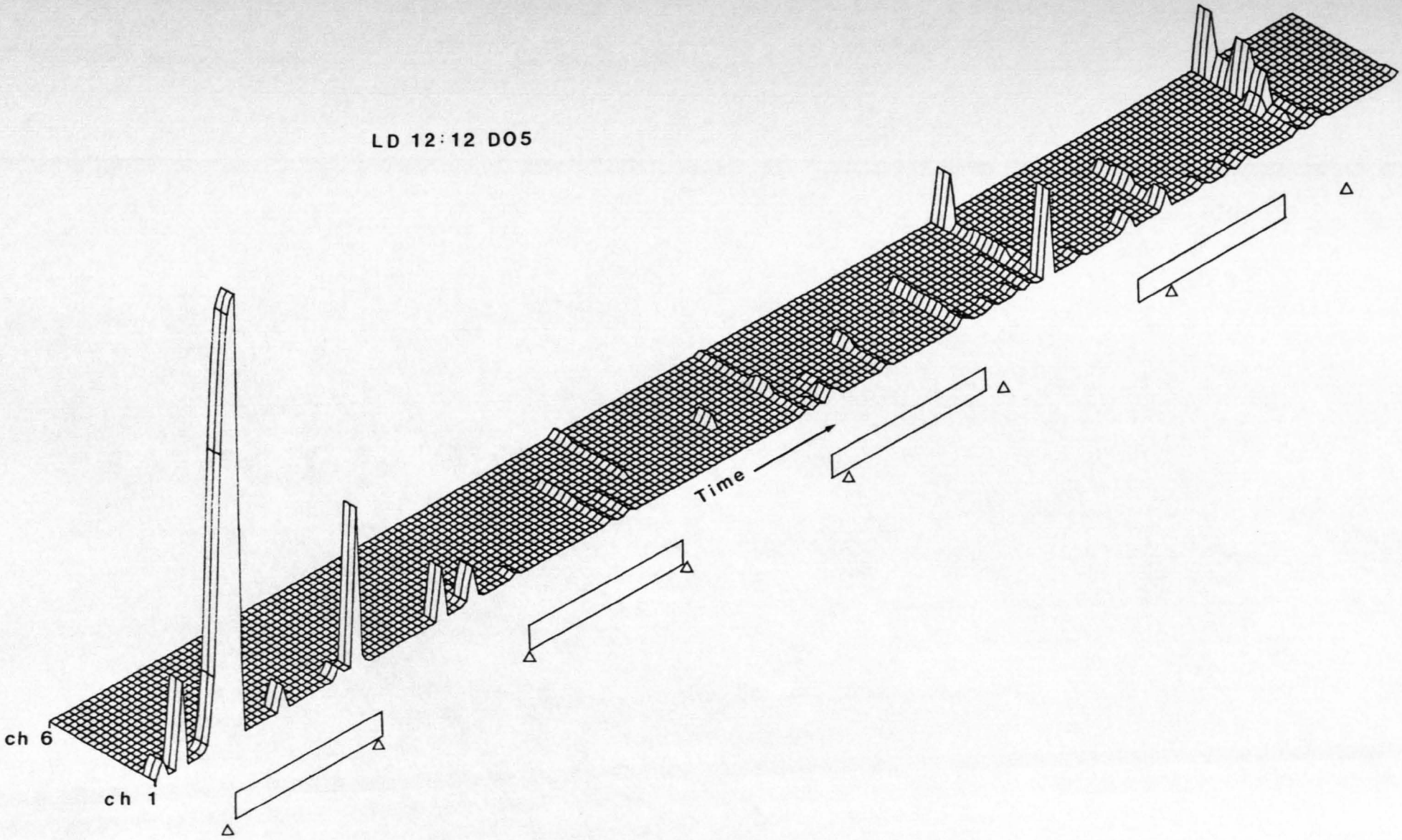

LD 12:12 D05
Time
ch 6
ch 1

Figure 3.32

3-dimensional plot of activity pattern shown by crab TD8 under constant darkness. This plot shows a very high overall level of activity, with activity occurring evenly throughout the experimental apparatus.

LD 00:24 TD8

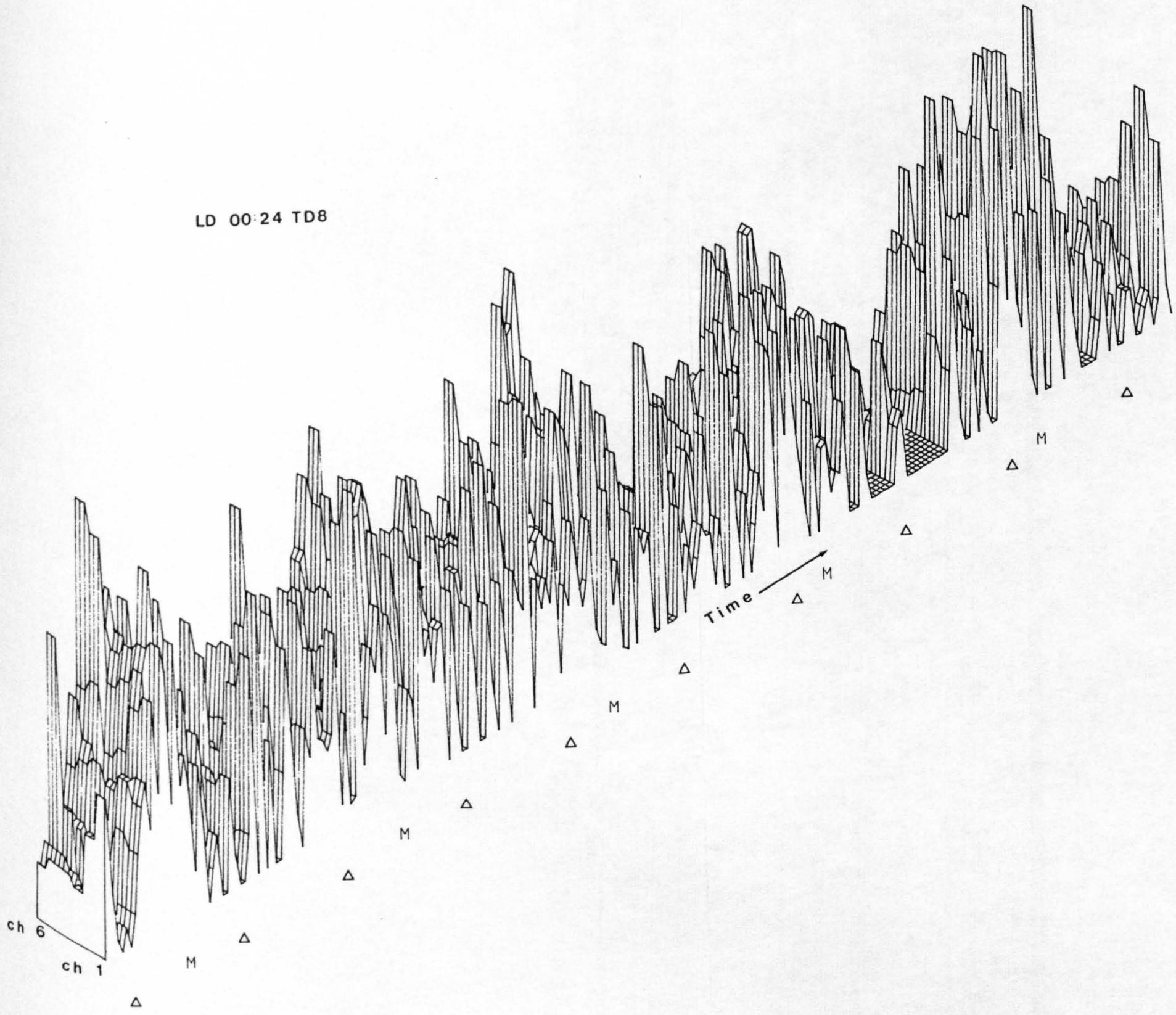
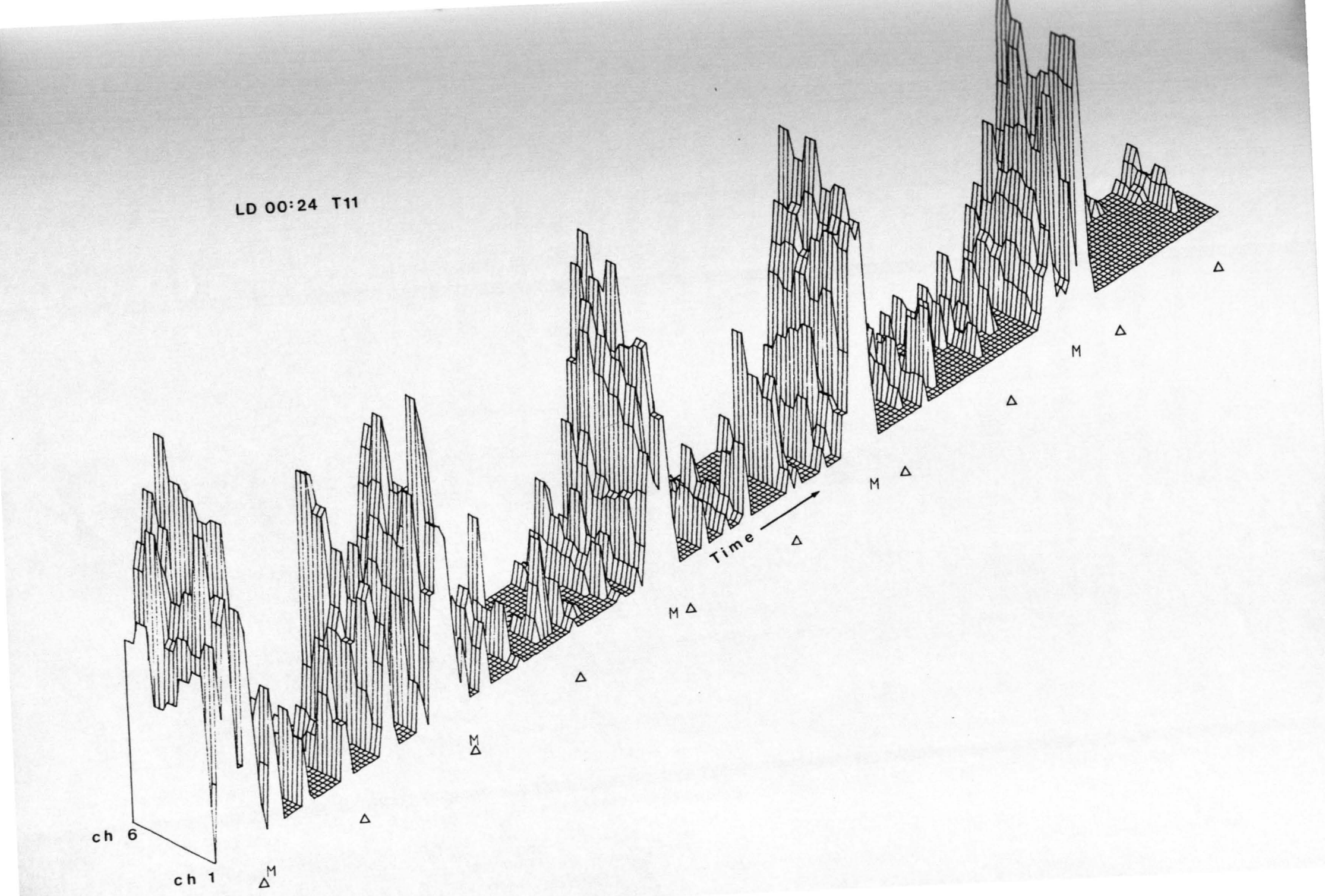


Figure 3.33

3-dimensional plot of activity pattern of crab T11 (LD 00:24) showing a clear cyclic component. The five major, evenly spaced peaks of activity correspond with 'expected' night-time, flood/high tide. Activity occurs evenly throughout the experimental apparatus.


LD 00:24 T11
Time
ch 6
ch 1
M

particular area of the tank, bursts of activity occurring evenly across all light beams. Unlike the three previous examples, this crab shows five major, evenly spaced peaks of activity during the five day experimental recording period. This corresponds to a 24 hour cycle of activity and closer examination of Figure 3.33 shows that these peaks occur during expected night time, co-inciding with expected high/flood tide.

The 3-dimensional plots therefore provide a quick visual check of activity over time. However, there was little evidence of irregular use of areas of the tank as shown in Figures 3.30 and 3.31. The channel Ø data were analysed and the results compared with those from the individual channels. In every case in which an animal displayed significant rhythmic locomotor activity on an individual channel, this was reflected on the overall activity channel, and a similar significant peak was detectable. The overall activity data (Channel Ø) therefore appears to be a perfectly adequate estimator of the activity displayed in the experimental tank.

3-3.3 STANDARD LABORATORY LIGHTING REGIME (LD 12:12)

The primary aim of this experimental regime was to investigate the locomotor activity displayed by L. depurator under normal laboratory conditions. Thirteen crabs were used and sex, size, place of capture and experimental identifications of each, are given in Appendix B (Table B.1)

Nine crabs (69%) did not show any statistically significant rhythmicity (Table 3.2). The significant periodicities shown by the other four crabs is summarised in Table 3.3. Two of the crabs D13 and D14 showed 25 hour cycles of activity (Figures 3.34 and 3.35 respectively) while DØ6 and DØ7 showed a six hour cycle and 12 hour cycle respectively (Figure 3.36 and Figure 3.37).

Both of the crabs showing a 25 hour cycle of activity were collected from the same shallow sub-littoral site at Loch Feochan. Examination of the plots of overall activity against time for both of these crabs (Figure 3.22; Figure 3.23) suggests a connection between activity peaks and times of 'expected' high or flood tides. Both crabs also show evidence of increased activity during periods of darkness and particularly at 'expected' night time high tide. There is also some suggestion of an increase in activity associated with the abrupt changes in light state. However, in both Figure 3.22 and Figure 3.23, times of expected high tide fall sufficiently close to the point of light transition to confuse the matter.

The other two crabs showing significant cyclic locomotor behaviour, were collected from a depth of 35 metres off the Isle of Cumbrae. The plots of activity against time (Figure 3.38, Figure 3.39) bear little resemblance to one another. Both plots however, do have activity peaks in both light and dark phases. Crab DØ7 showed a 12 hour cycle of activity (Figure 3.37) and examination of Figure 3.39 shows quite clearly that peaks of activity are closely associated with change in light state. The situation however, is further complicated as times of expected high tides occur in close proximity to points of light transition. This situation is similar to that shown in Figure 3.22 and Figure 3.23 above.

Table 3.2
Results obtained from 13 crabs maintained individually under LD 12:12 lighting conditions in the laboratory.

		Capture site	
Number of crabs showing cyclic locomotor activity	4 (31%)	I. of Cumbrae	2
		Loch Feochan	2
Number of crabs showing random locomotor activity	9 (69%)	I. of Cumbrae	9
	N=13		

Table 3.3
Table showing periodicity of cycles displayed under LD 12:12 lighting conditions.

Experimental Identification	Periodicity of activity cycle
D06	6 hour
D07	12 hour
D13	25 hour
D14	25 hour

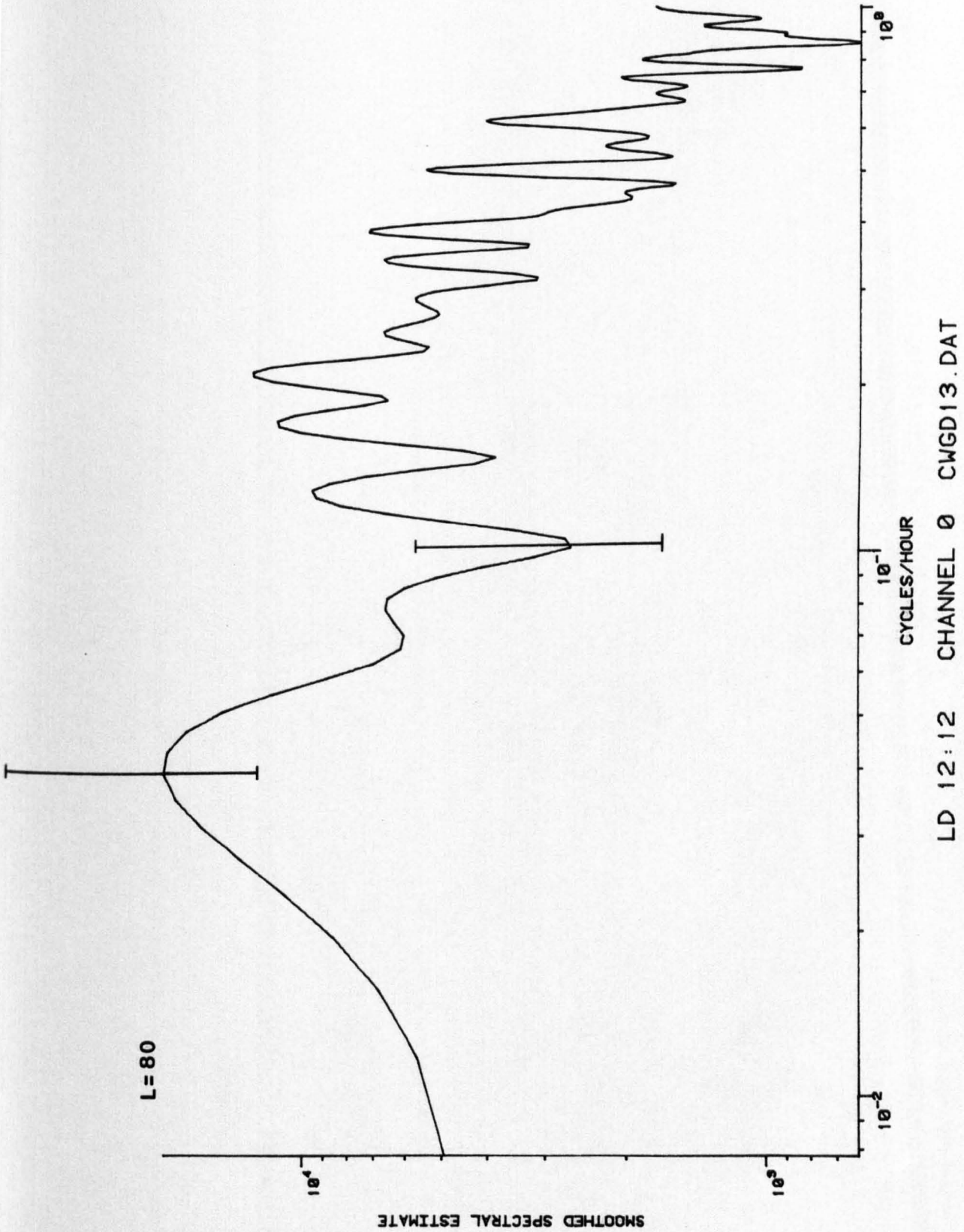


Figure 3.34
Smoothed spectral estimate showing single significant peak corresponding to a 25 hour cycle.

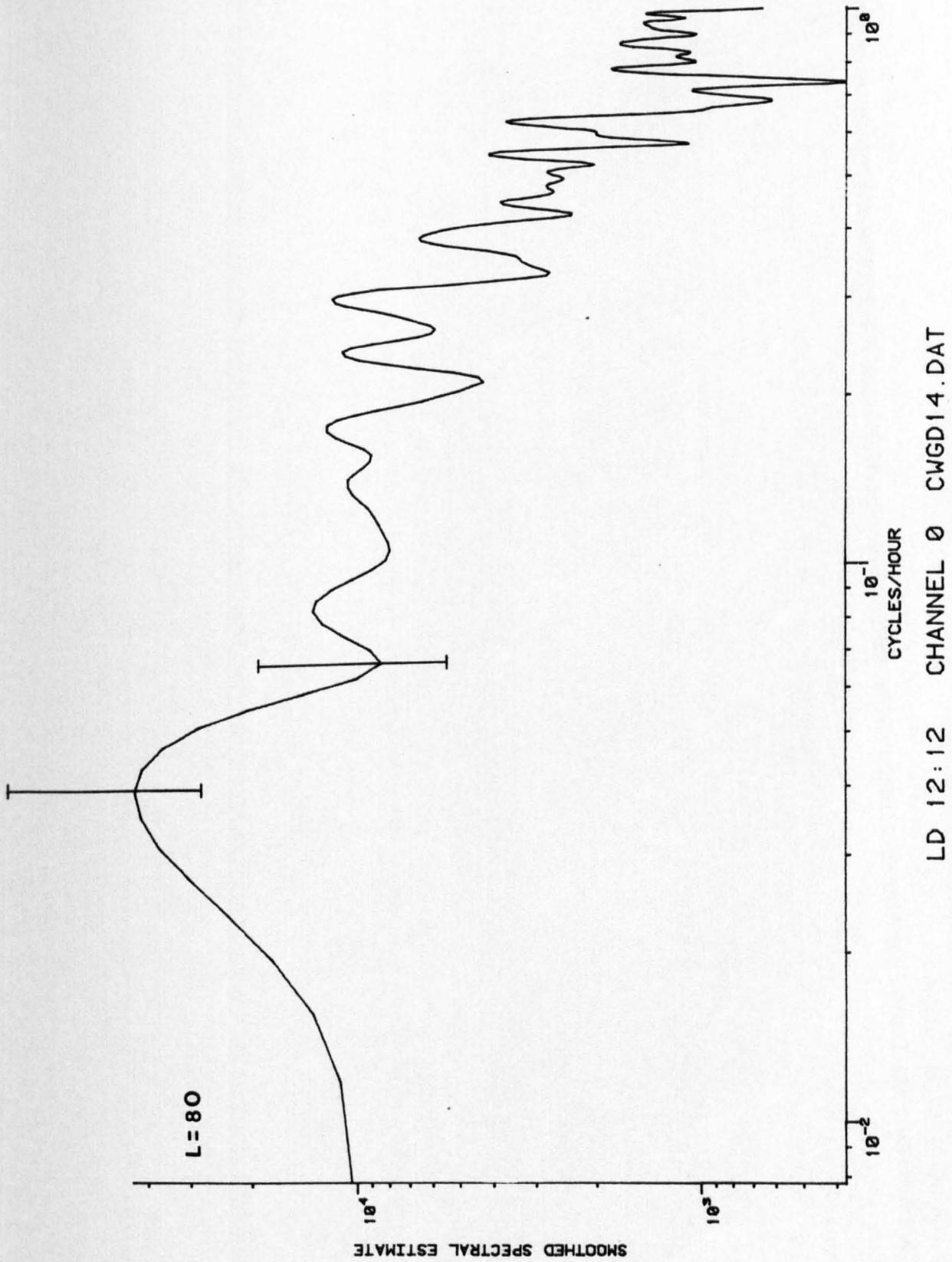


Figure 3.35
Smoothed spectral estimate showing a single significant peak corresponding to a 25 hour cycle.

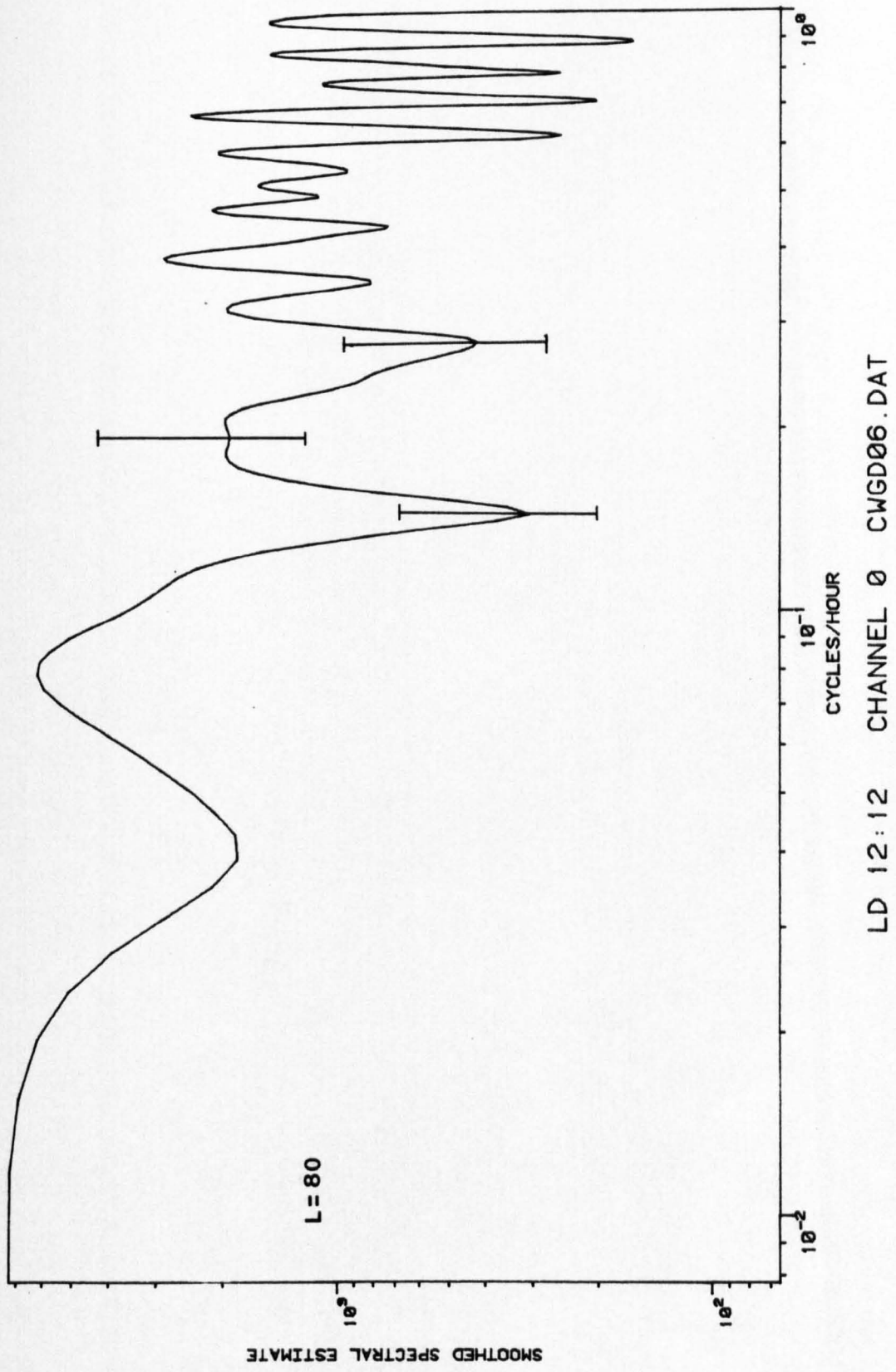


Figure 3.36
Smoothed spectral estimate showing a single significant peak corresponding to a 6 hour cycle.

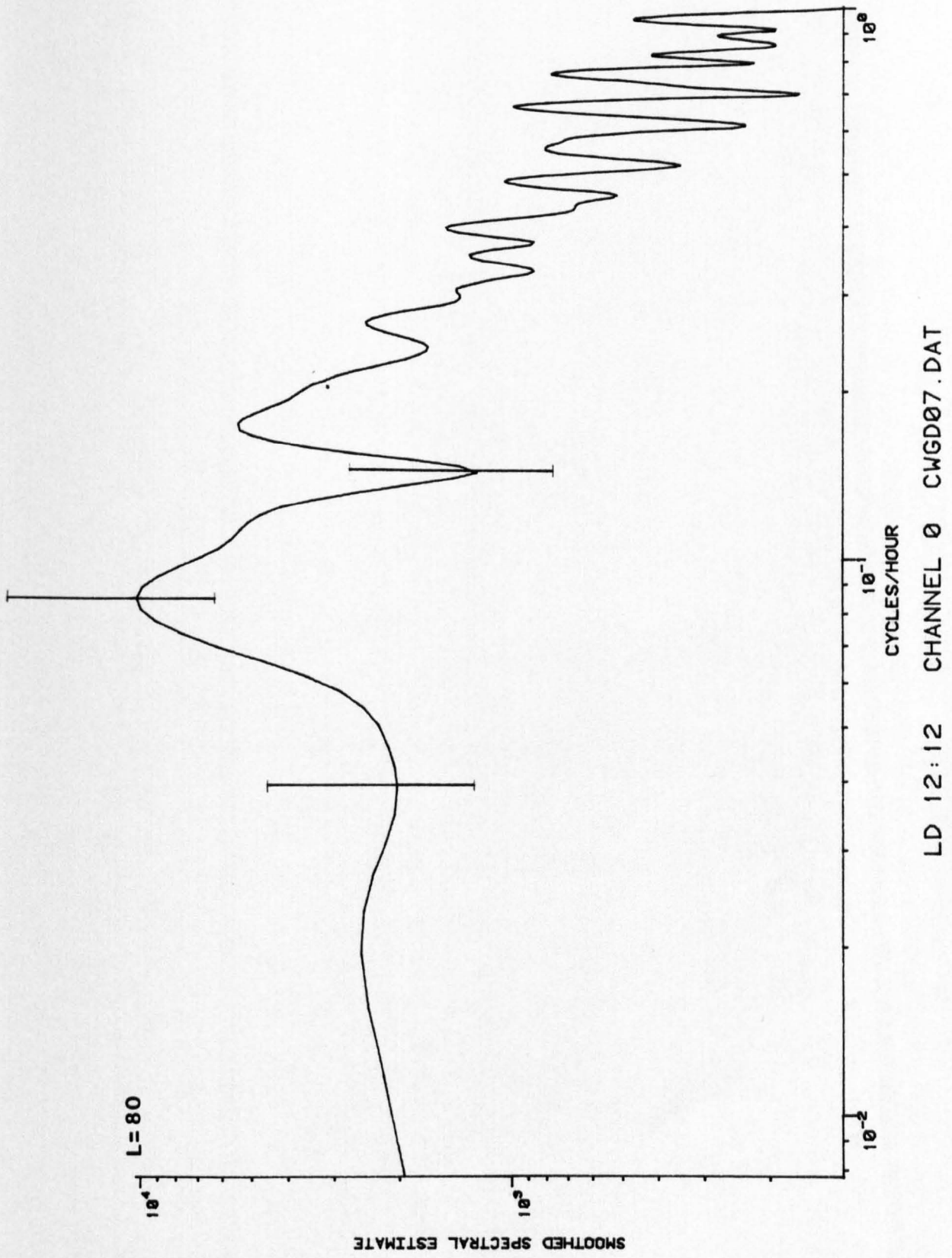


Figure 3.37
Smoothed spectral estimate showing a single significant peak corresponding to a 12 hour cycle.

Figure 3.38
Plot of activity against time for crab D06.

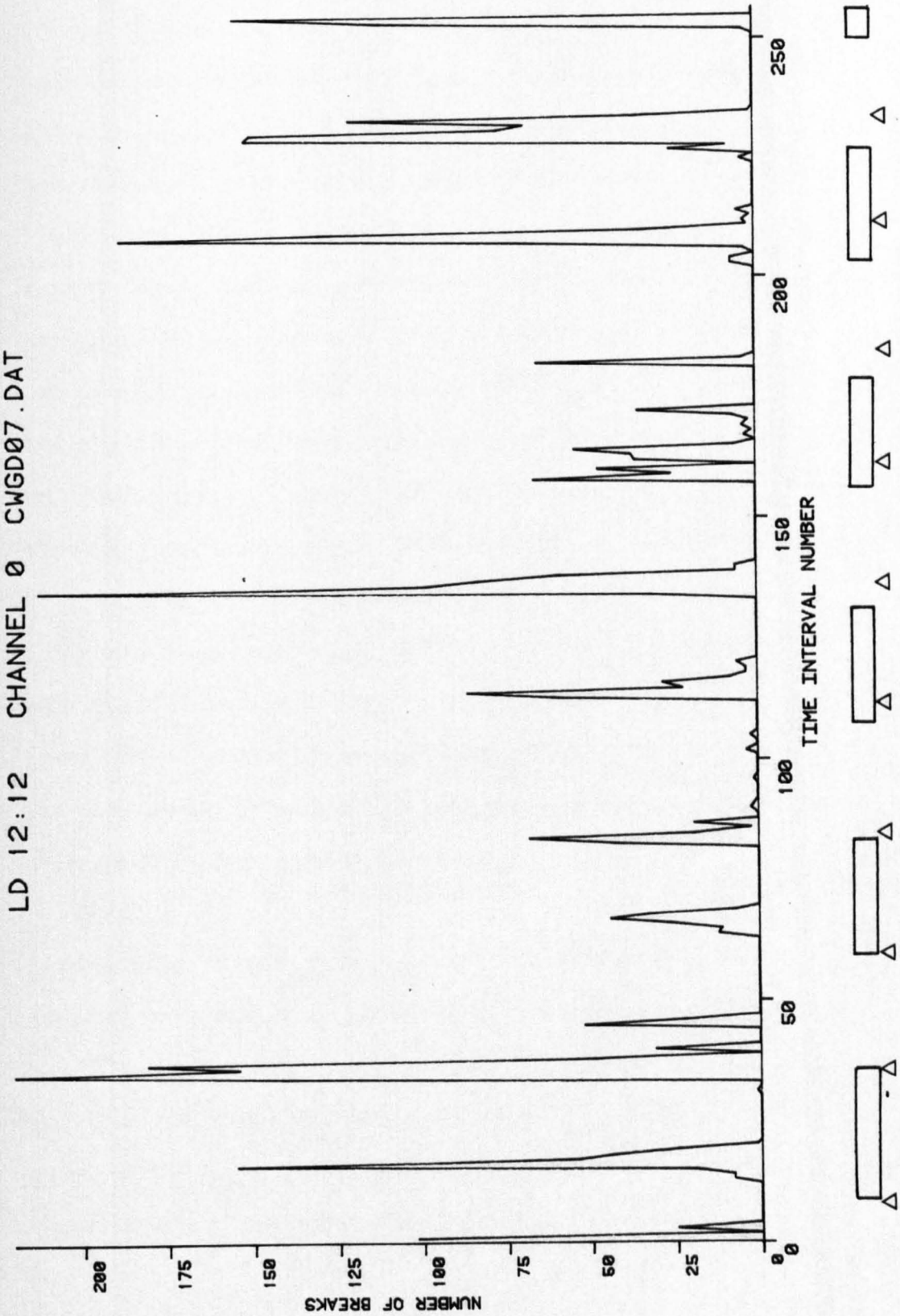


Figure 3.39
Plot of activity against time for crab D07.

The results obtained from crab DØ6 are more difficult to explain. The plot of activity against time (Figure 3.38) shows activity in both light and dark phases of the light cycle, but unlike the three examples quoted above, there is little evidence of peak activity coinciding with either 'expected' high tide or transition of light state. In addition, visual examination of Figure 3.38 and the 3-dimensional plot of activity (Figure 3.40) suggests little evidence of cyclic locomotor behaviour. Further examination of the smoothed spectral estimate of the data (Figure 3.36) shows that the significant peak is very wide and may best be described as a plateau rather than a peak. This may have been formed by close proximity of two separate peaks in the smoothed spectral estimate. If this is the case, the peak then ceases to be significant and the smoothed spectral estimate for this time series is no longer significantly different from the smoothed spectral estimate of random data. Although slightly unsatisfactory, this peak was taken as representing a significant periodicity of 5.5 hours for the purposes of this study. No other plateau similar to this was observed during the course of the study.

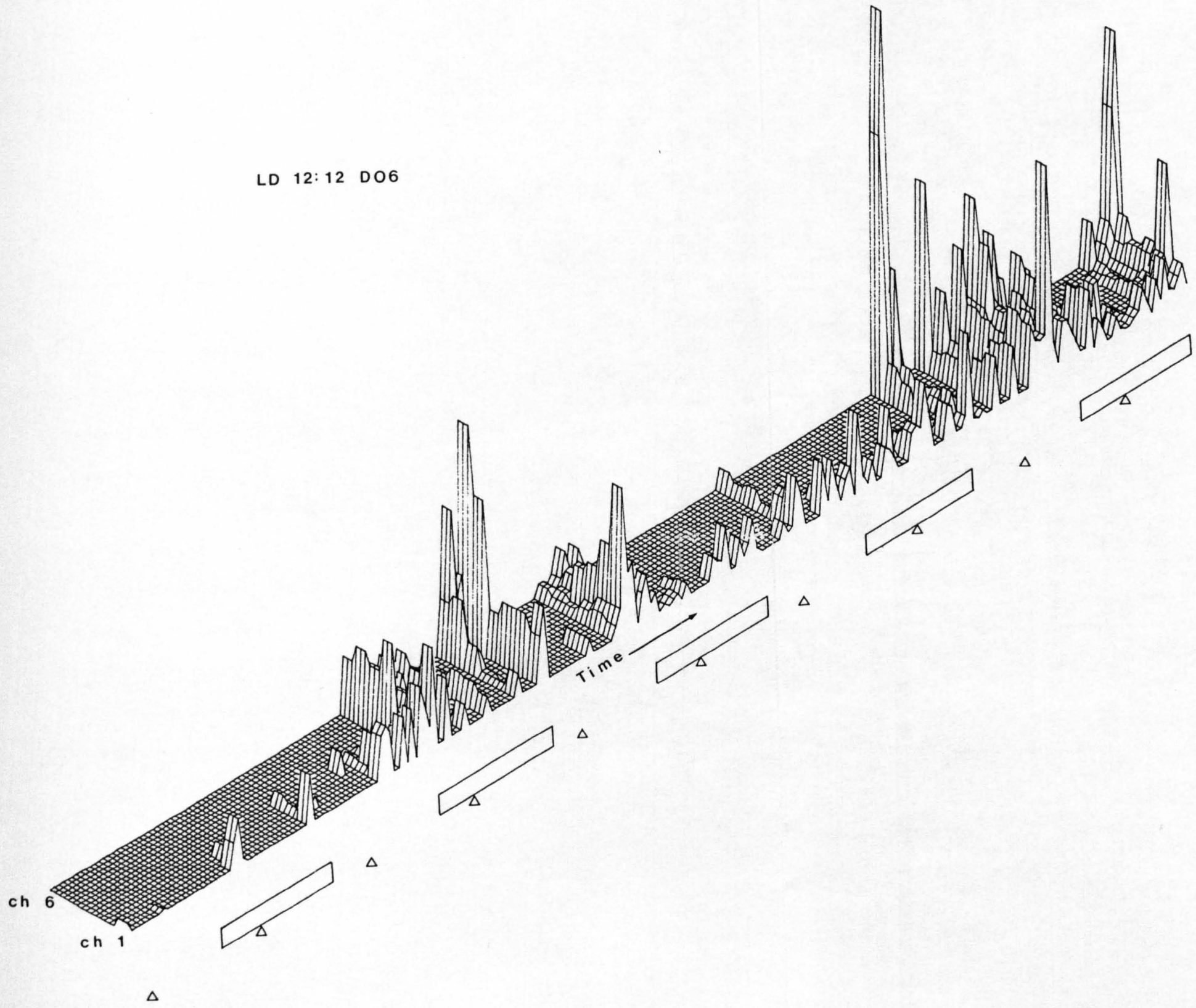
Eleven of the thirteen crabs used in this experimental regime were collected from deep water off the Isle of Cumbrae (Table 3.2). Only two of these deep water crabs showed rhythmic locomotor behaviour. The other nine crabs showed apparently random activity during the course of the experiments, with no obvious activity corresponding to either changes of light state or to times of 'expected' high tide.

The above results, while not conclusive, show that at least some of the swimming crabs display significant, cyclic activity under LD 12:12 conditions. In three of the four crabs showing cyclic behaviour,

Figure 3.40

3-dimensional plot of activity shown by crab DØ6 housed under LD 12:12 lighting conditions.

LD 12:12 D06



there is evidence to suggest that some of the activity may correspond either with the dark phase of the lighting regime, or with the transition between light states. The possibility therefore existed that cyclic locomotor behaviour may have been induced in some crabs by the cyclic laboratory environment. In order to investigate this, the cyclic aspect of the laboratory environment was removed and similar experiments carried out in both constant light and constant darkness conditions.

3-3.4 CONSTANT ILLUMINATION (LD 24:00)

In this regime, animals were maintained under conditions of constant illumination, lighting being provided by fluorescent tubes, colour balanced for daylight. Seven individual crabs were studied and relevant identification information is given in Table B.1 (Appendix B). Four of these seven crabs showed random locomotor behaviour, and Table 3.4 summarises the results obtained under this regime. The two crabs collected from the shallow sub-littoral site at Loch Feochan, both show significant cyclic activity. Crab TØ6 shows a clear 25 hour cycle of activity (Figure 3.41). Examination of the 3-dimensional activity plot (Figure 3.42) shows immediately that activi ty peaks are very closely associated with 'expected' night time flood/high tide.

Crab TØ7 and crab TØ4 show activity patterns which are less easy to explain. They show significant cycles of 28 hours and 8 hours respectively (Figure 3.43, Figure 3.44). Figure 3.45 shows the three

Table 3.4

Summary of results obtained under constant illumination conditions (LD 24.00).

	Collection site	Frequency of cycle	Experimental identification	Total
Crabs showing cyclic locomotor activity	Isle of Cumbrae	8 hour	T04	
	Loch Feochan	25 hour	T06	3
	Loch Feochan	25 hour	T07	
Crabs showing random activity	Isle of Cumbrae	---	T01	
	Isle of Cumbrae	---	T02	4
	Isle of Cumbrae	---	T03	
	Isle of Cumbrae	---	T05	

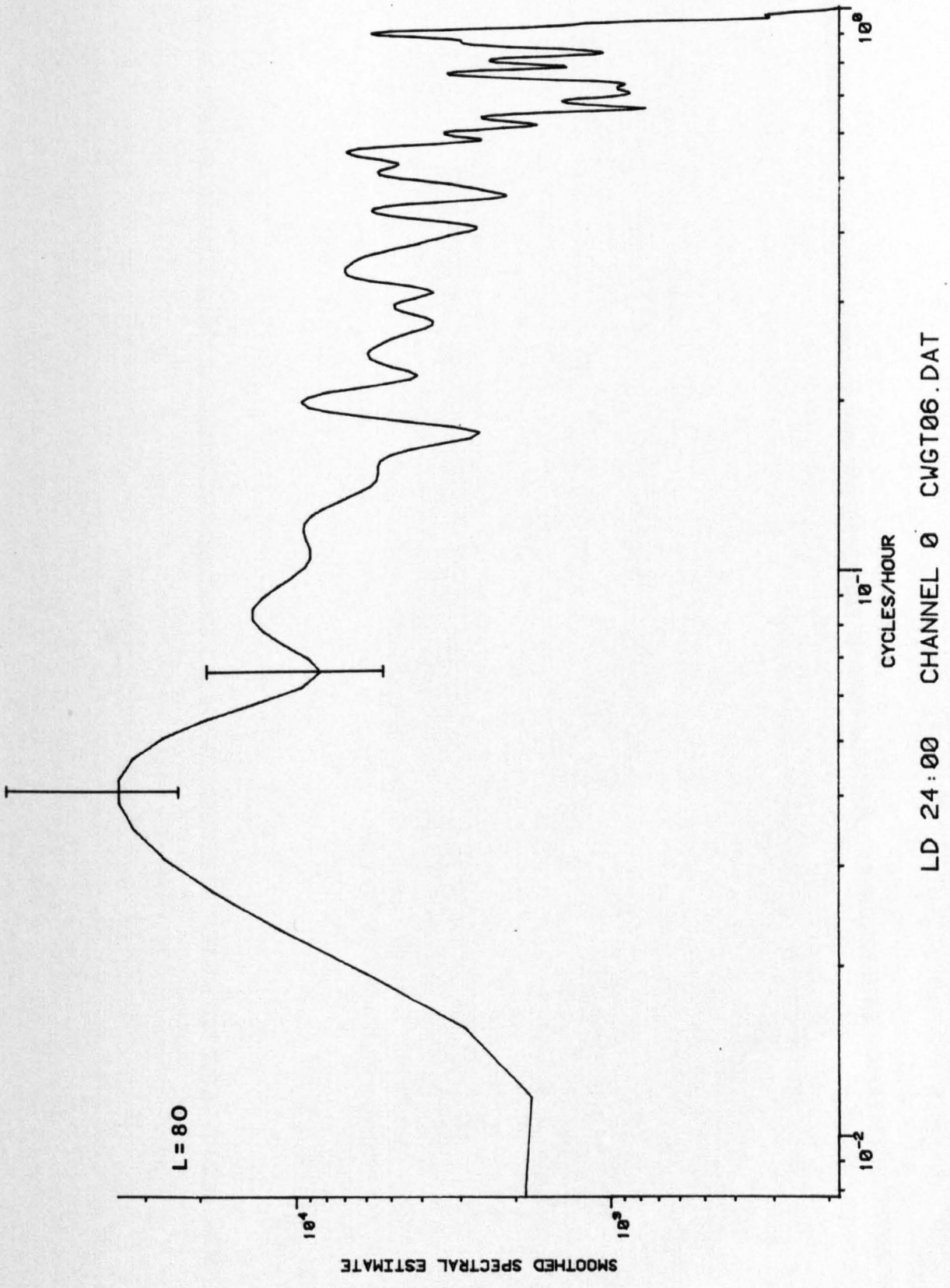
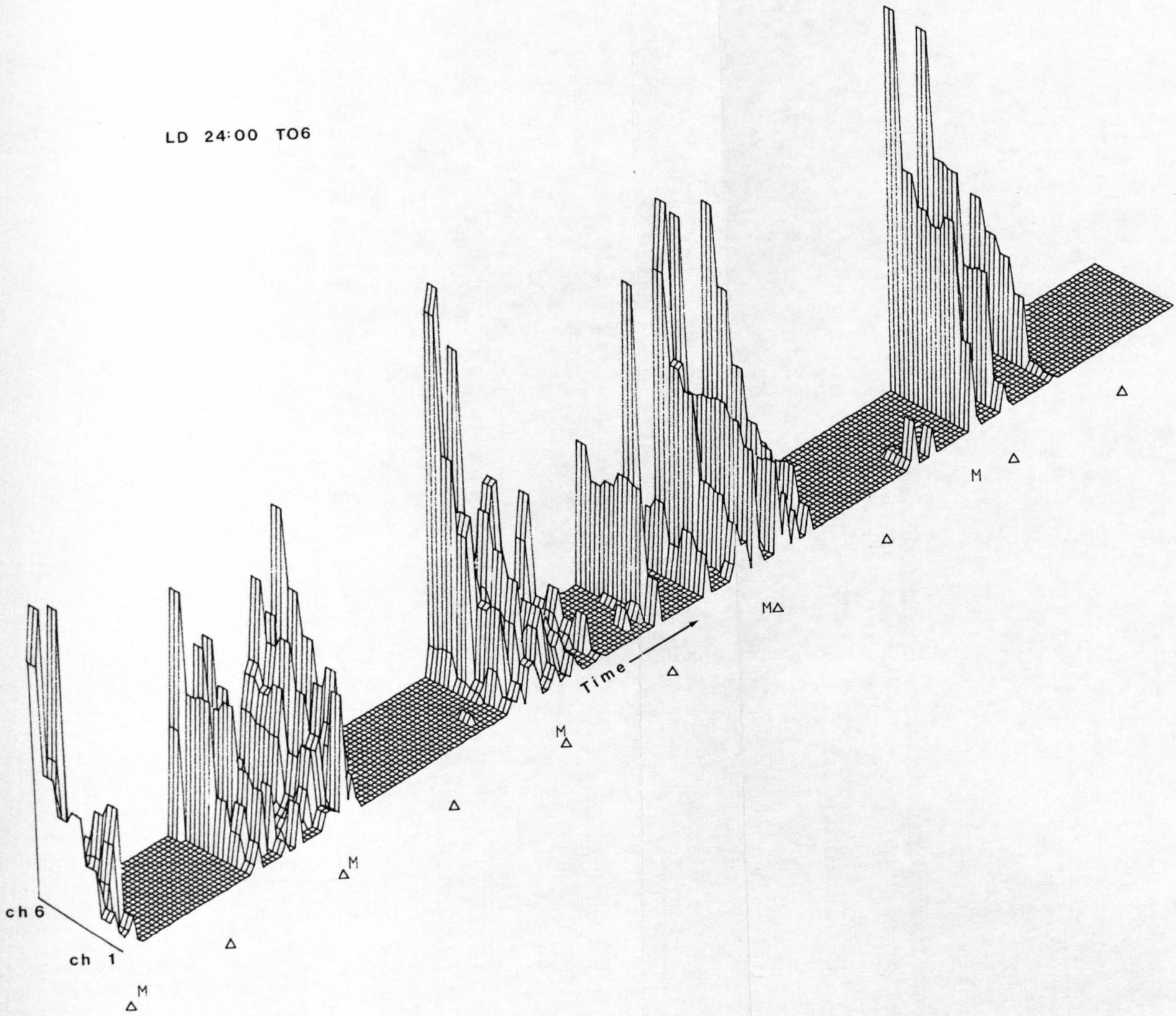


Figure 3.41
Smoothed spectral estimate showing a single significant peak corresponding to a 25 hour cycle.

Figure 3.42

3-dimensional plot of activity displayed by crab TØ6 housed under constant illumination (LD 24:00).

LD 24:00 TO6



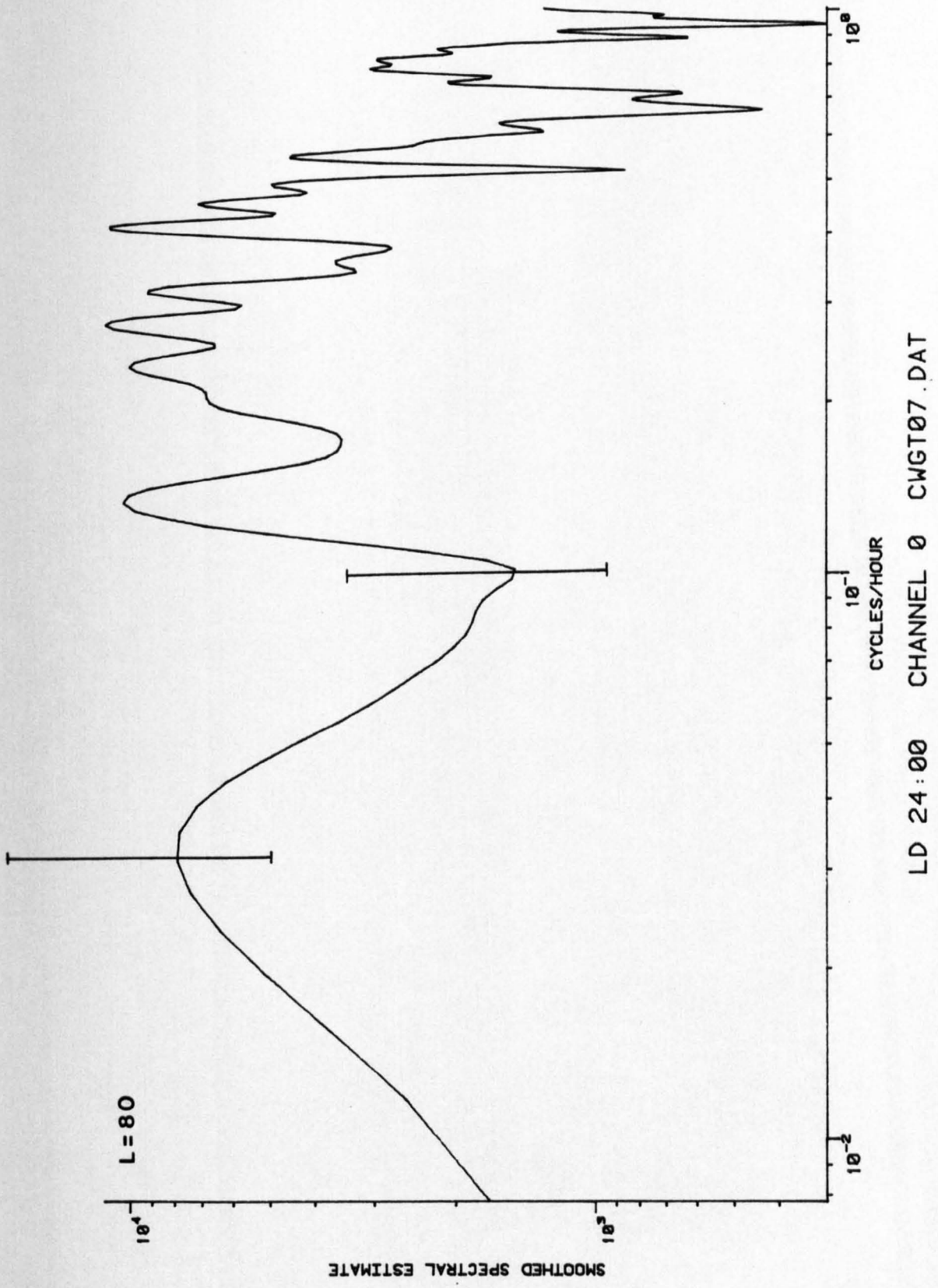


Figure 3.43
Smoothed spectral estimate of a time series showing a 28 hour cycle of activity.

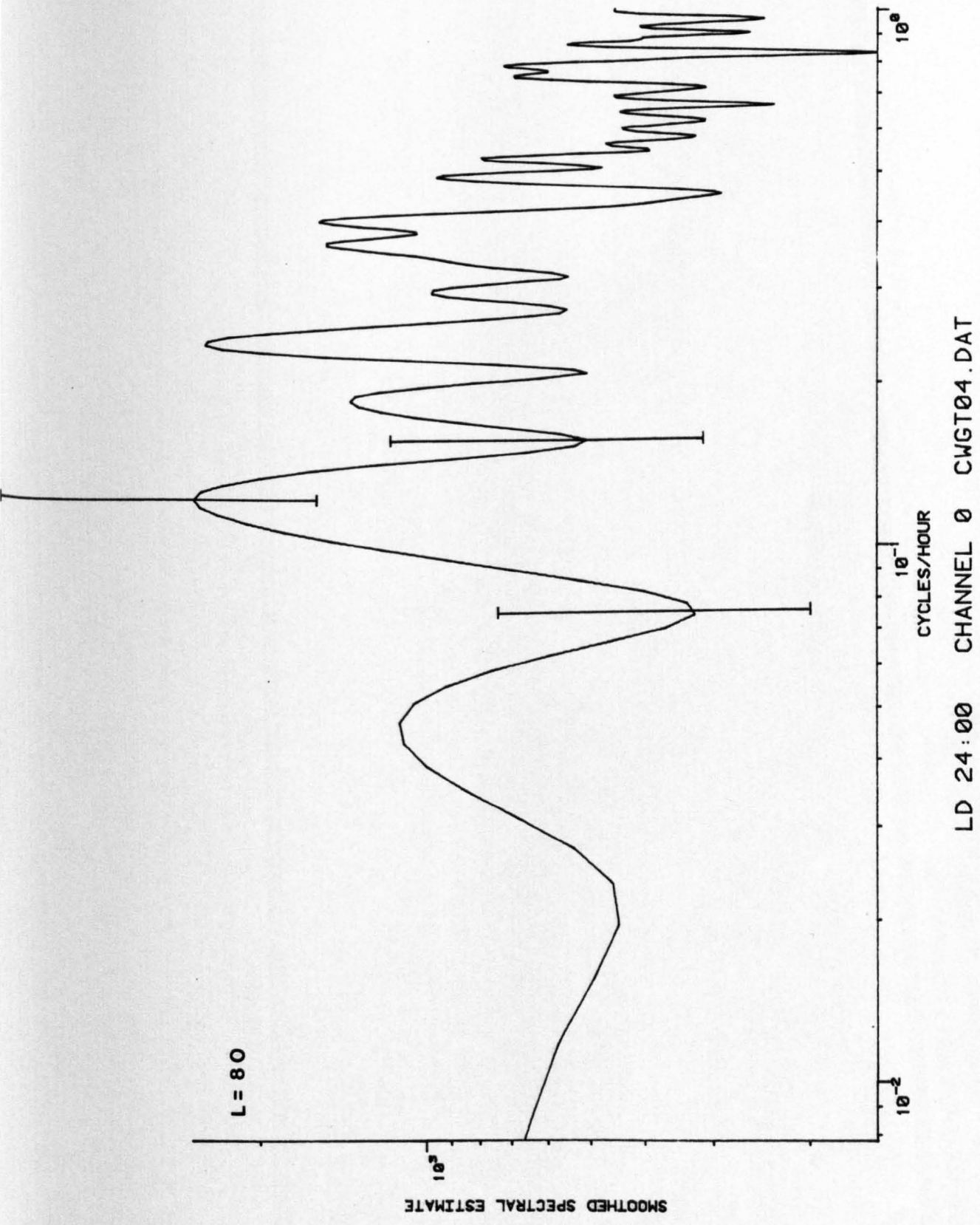
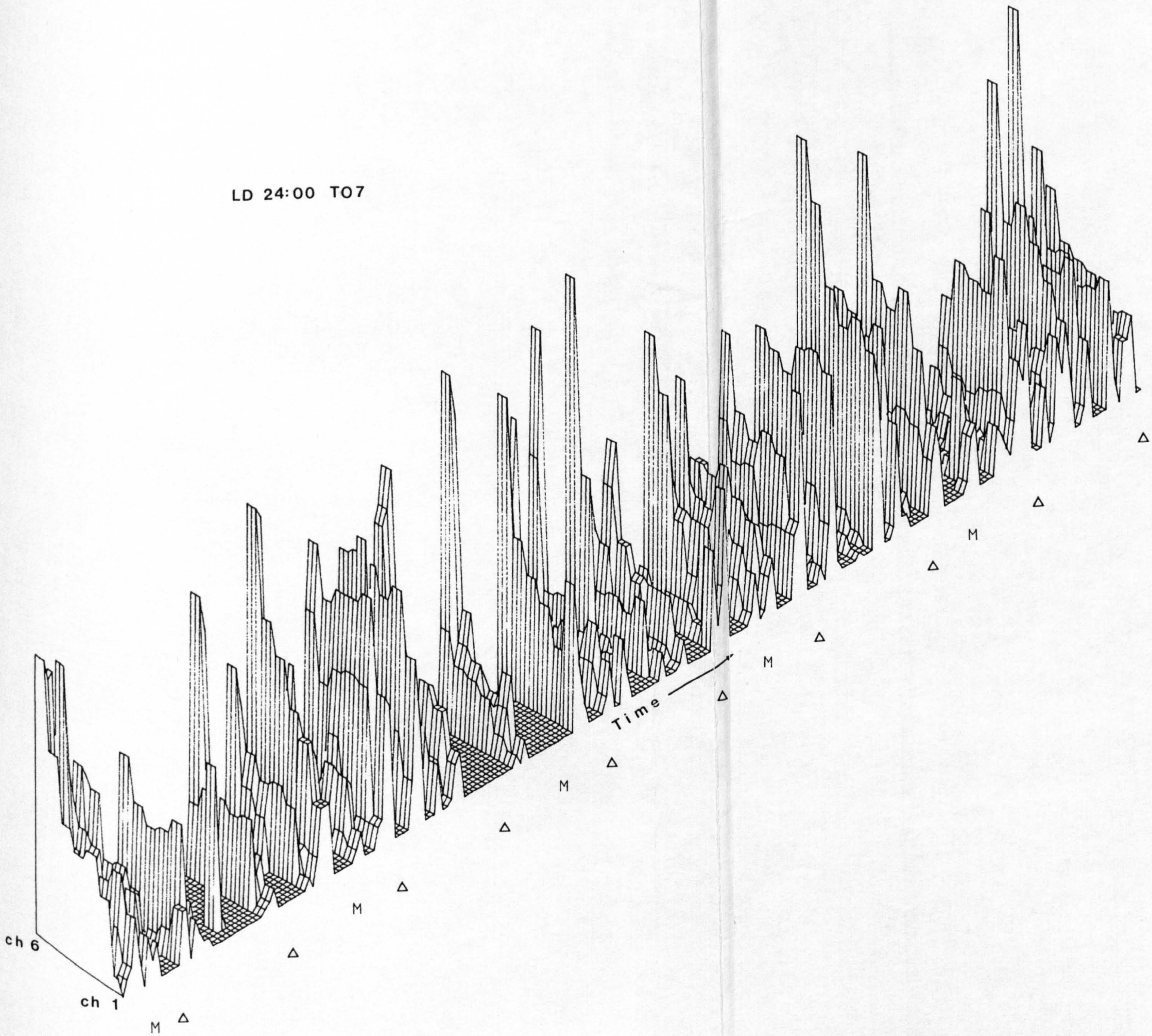


Figure 3.44
Smoothed spectral estimate of time series data obtained from crab T04. This shows a single significant peak corresponding to an 8 hour cycle of activity.

Figure 3.45

3-dimensional plot of activity shown by crab TØ7 (LD 24:00). This plot shows a high level of overall activity with few irregularly spaced periods of inactivity and no obvious association between activity and 'expected' high tide or 'expected' night time.


LD 24:00 TO7
Time
ch 6
ch 1
M

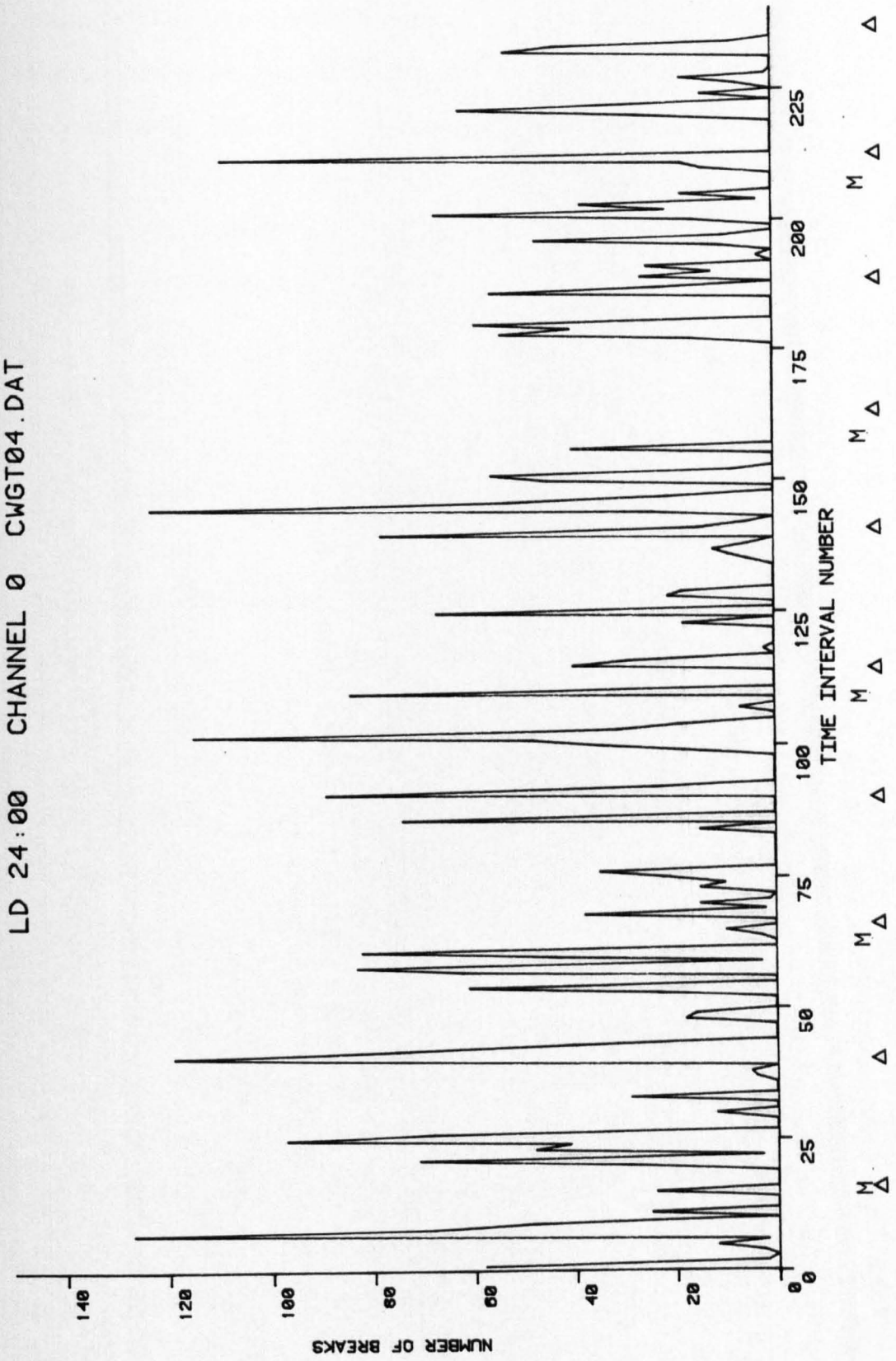


Figure 3.46
Plot of activity against time for crab T04.

dimensional plot of activity displayed by crab TØ7 while Figure 3.46 shows total activity against time for crab TØ4. Examination of these figures indicates that both animals show high levels of overall activity with very few irregularly spaced periods of inactivity. Further inspection of Figures 3.45 and 3.46 reveals no immediately obvious association between activity and either time of 'expected' high tide or 'expected' night time.

3-3.5 CONSTANT DARKNESS (LD 00:24)

Table 3.5 summarises the results obtained from the 14 crabs observed under this regime. Six crabs showed significant cyclic locomotor activity, while eight showed activity with no cyclic component. The six crabs showing cyclic activity were all collected from shallow sub-littoral sites at Loch Feochan and Loch Sween. Of the six crabs collected from deep water (>30 metres) off the Isle of Cumbrae, none showed cyclic activity patterns.

Figure 3.47 shows the activity of crab TD5 obtained from the Isle of Cumbrae. This shows a high level of activity over the entire recording period with no obvious correlation between activity and time of 'expected' high tide or 'expected' night time. Not all crabs from Isle of Cumbrae showed such high levels of activity as TD5, but in all of them, activity occurred uniformly throughout the recording period.

Table 3.5

Summary of results obtained under constant darkness conditions (LD 00:24).

	Collection site	Frequency of cycle	Experimental identification	Total
Crabs showing locomotor rhythmicity	Loch Feochan	7 hour	TD9	6
	Loch Feochan	25 hour	TD11	
	Loch Sween	25 hour	TD3	
	Loch Sween	7 hour	TD7	
	Loch Sween	25 hour	TD13	
	Loch Sween	25 hour	TD14	
Crabs showing no locomotor rhythmicity	Loch Feochan (2)	---	TD8, TD10	8
	Isle of Cumbrae (6)	---	TD5, TD1 TD6, TD0 TD2, TD4	

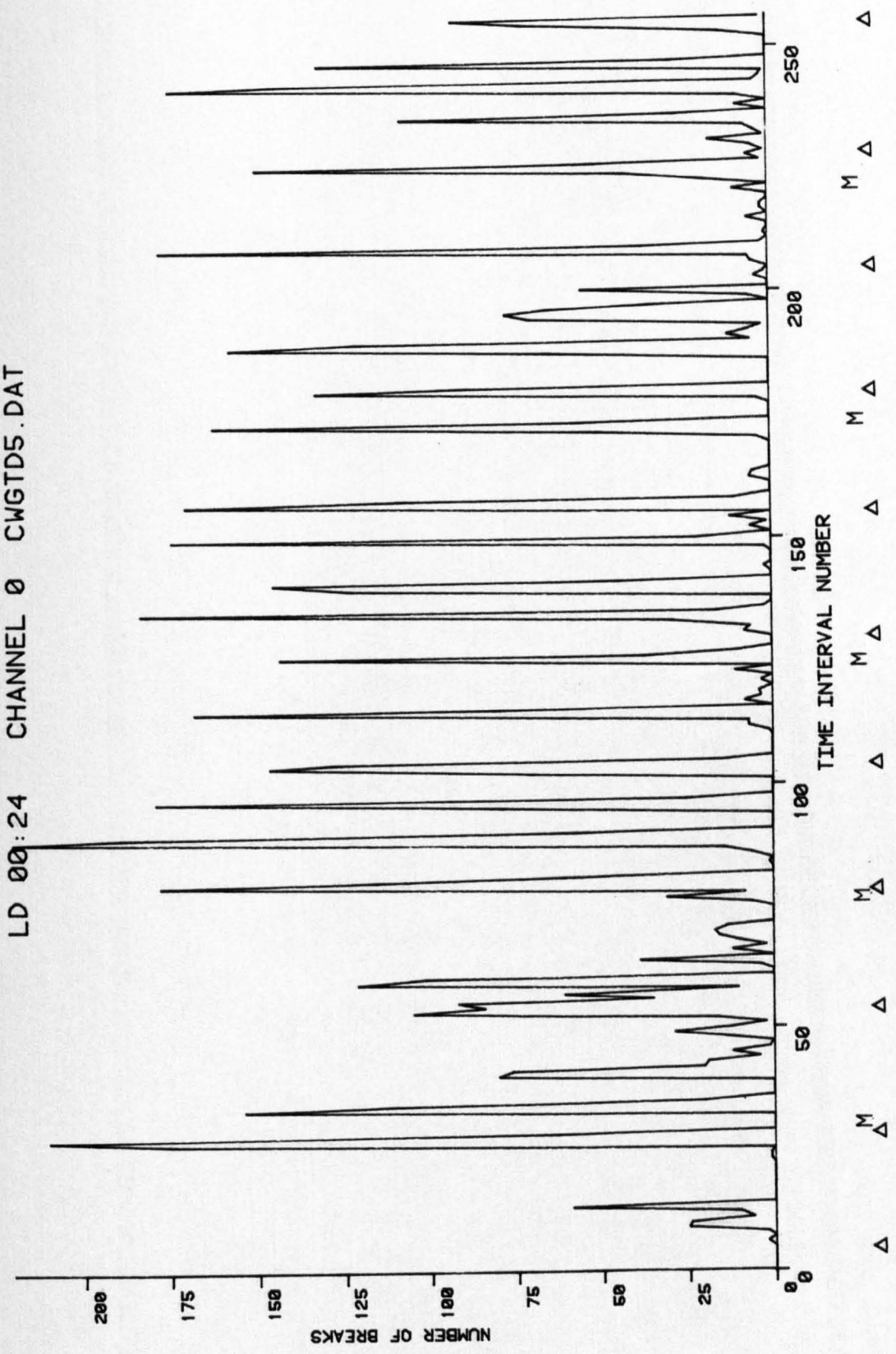


Figure 3.47
Plot of activity against time for crab TD5.

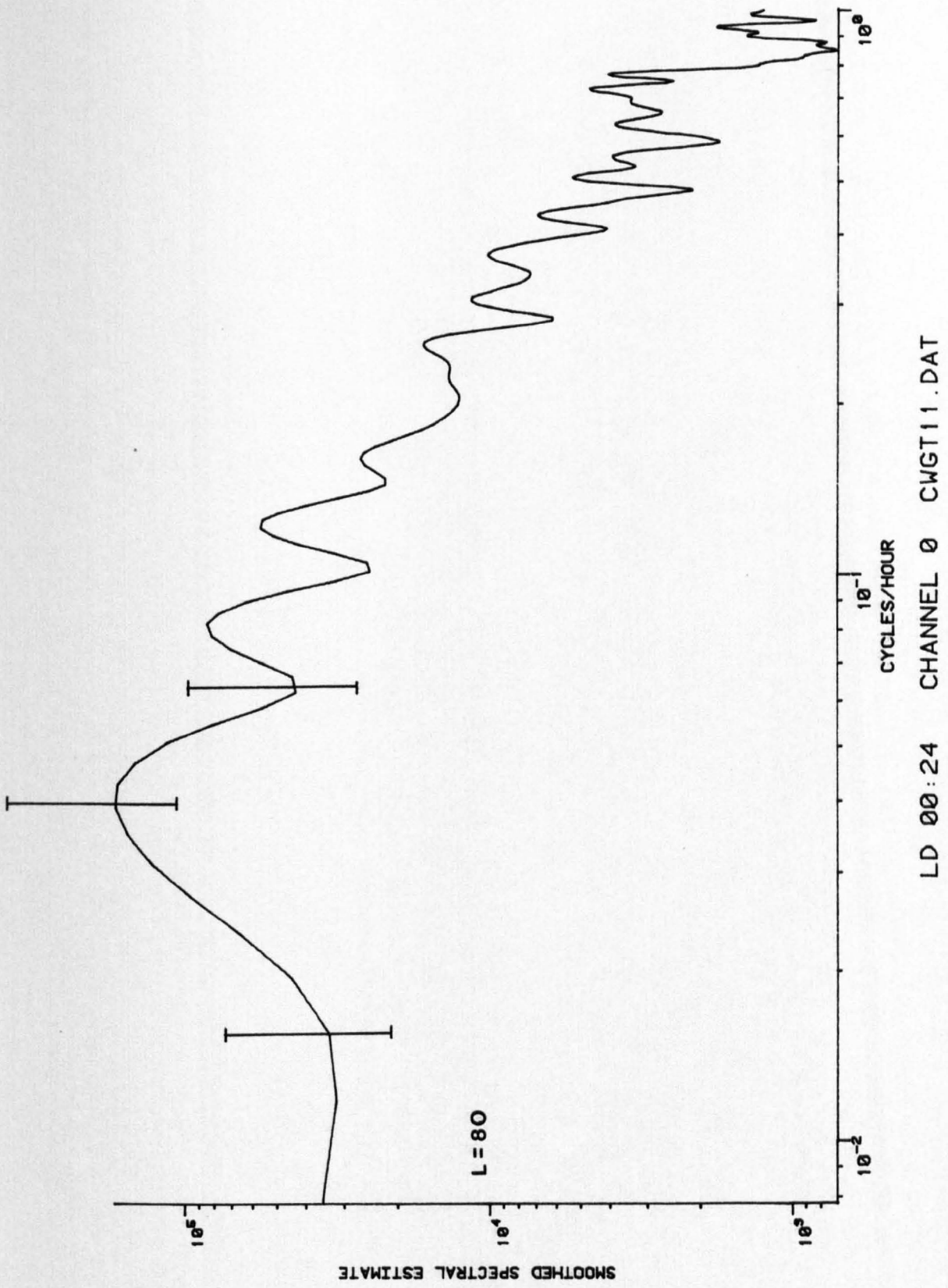


Figure 3.48
Smoothed spectral estimate of activity shown by crab TD11 indicating a 25 hour cycle of activity.

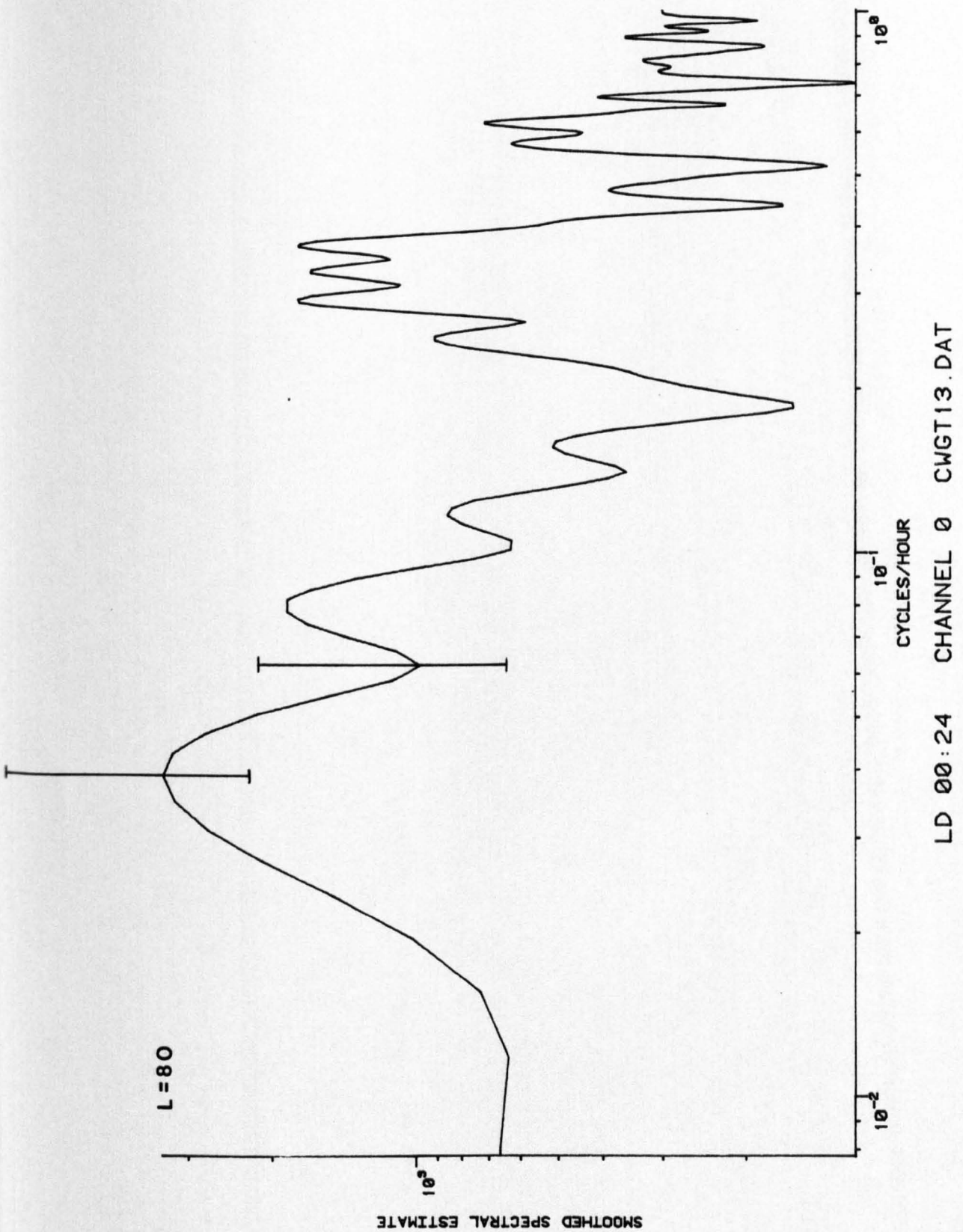


Figure 3.49
Smoothed spectral estimate showing a significant peak corresponding to a 25 hour cycle of activity.

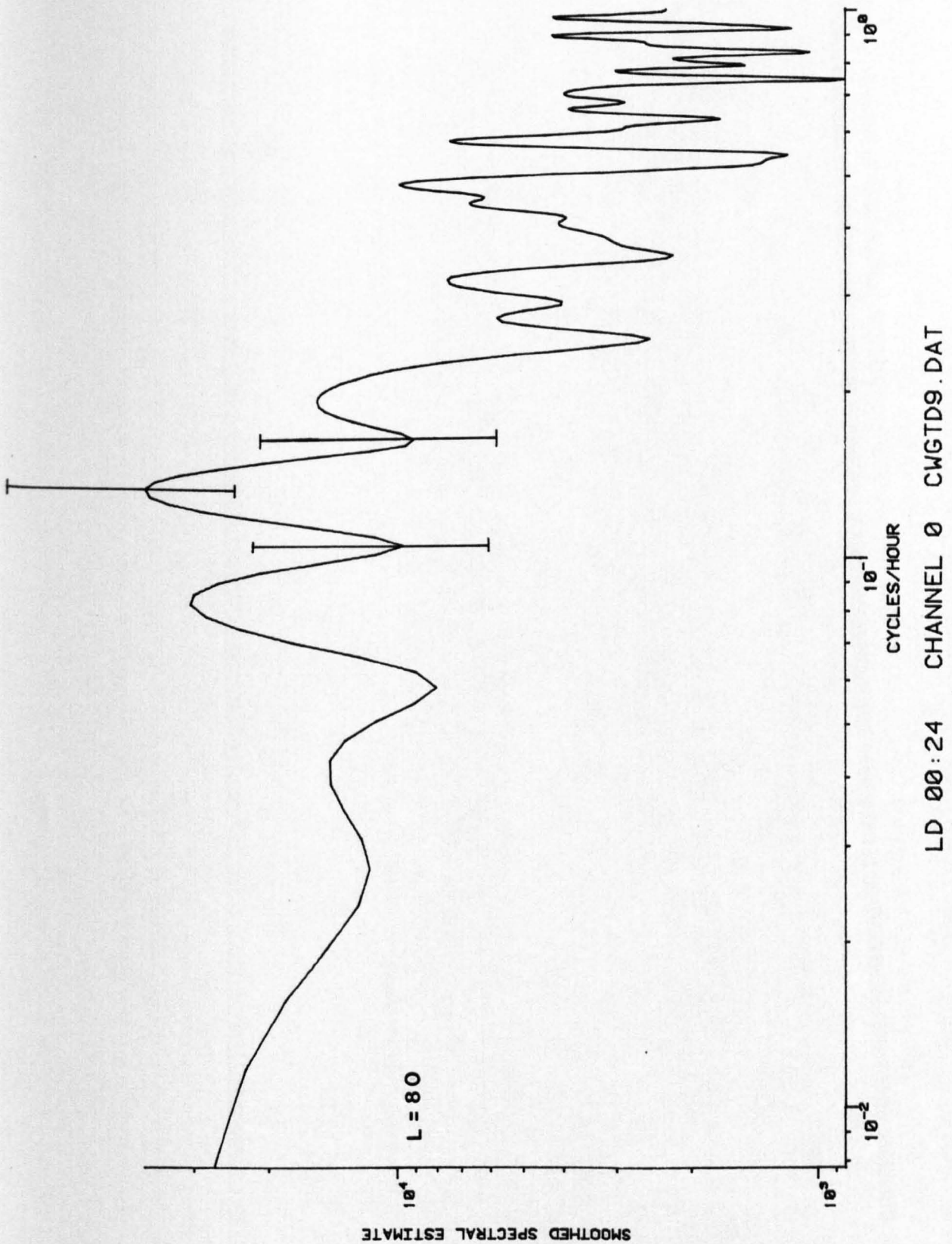


Figure 3.50
Smoothed spectral estimate showing a 7 hour periodicity.

Table 3.6

Summary of cyclic locomotor activity shown by crabs at each collection site.

Collection site	Number of crabs	Number showing cyclic locomotor activity	Periodicities present
Isle of Cumbrae (>30m)	22	3(14%)	8 hour 6 hour 12 hour
Loch Feochan (3-9m)	8	6(75%)	7 hour 28 hour 4 x 25 hour
Loch Sween (3-9m)	4	4(100%)	4 x 25 hour

Of the six crabs showing significant rhythmic behaviour, five show 25 hour cycles and one shows a peak in the smoothed spectral estimate corresponding to a seven hour cycle. Smoothed spectral estimates of TD11 and T13 (Figure 3.48 and Figure 3.49) show single significant peaks corresponding to periodicities of 25 hours present in the data. Examination of 3.28 and Figure 3.33 shows quite clearly that peak activity occurs during periods of 'expected' night time. Initially, these peaks also occur at periods of flood/high tide.

Figure 3.29 is less clear. This animal was collected from the shallow sub-littoral zone at Loch Sween. Activity peaks occur between midnight and noon but in this case they also occur mid-way between 'expected' high tides. This was the only crab which showed a 25 hour cycle under this regime, in which activity did not correspond closely to 'expected' night time flood/high tide.

Crab TD9 was the only shallow water crab in this experiment in which the periodicity was not 25 hours. The smoothed spectral estimate (Figure 3.50) shows a single significant peak corresponding to a 7 hour cycle. Examination of the data from which the smoothed spectral estimate was calculated (Figure 3.27) however shows that activity occurs at all points in the tidal cycle. A seven hour cycle could be explained by activity occurring approximately at high and low tides; however, this type of activity pattern is not immediately obvious from Figure 3.27. The activity shown by this particular animal also differs from the others in this group in that peaks occurring at 'expected' night time are not larger than those during 'expected' daylight. Of the two shallow sub-littoral crabs which did not show rhythmic locomotor behaviour, one remained totally

inactive while the other (Figure 3.32) displayed hyperactivity throughout the entire recording period.

Table 3.6 summarises the results obtained in this investigation with out regard as to the lighting regimes employed. Ten of the twelve crabs collected from shallow sub-littoral sites (83%) exhibited significant rhythmic locomotor activity. Of the ten crabs showing rhythmicity, eight showed significant 25 hour cycles with one crab showing a seven hour cycle and one showing a 28 hour cycle.

Twenty two crabs were collected from deeper water off the Isle of Cumbrae. Only three (14%) of these crabs showed rhythmicity. No consistent pattern was apparent in these animals, a different periodicity being shown by each of the three crabs. These periodicities are shown in Table 3.6.

3-4 DISCUSSION

3-4.1 ACCLIMATISATION

The behaviour of the crabs during the 24 hour acclimatisation period showed much variability. The crabs used in this study were collected individually with no attempt to standardise time of capture, or to capture animals at a standard phase in the tidal cycle, therefore if the crabs show cyclic locomotor activity, the phase of the cycle may vary with respect to the start time of the experiment. This adds an extra complication to the analysis of the acclimatisation data, but may in part explain the considerable individual variation. The initial inactivity of crab TØ6 (Figure 3.16) may correspond to a natural period of inactivity, indicating that this animal has acclimatised to the experimental apparatus almost immediately. Similarly, the high initial activity displayed by T11 (Figure 3.20) for example, may not be due to either collection induced stress or the novel environment, but may represent a natural period of increased locomotor activity. If this is the case, then this particular crab has also acclimatised rapidly.

However, five of the eight crabs show a higher level of activity during the first eight hours of acclimatisation than at any other point in the experiment. In addition, all the crabs show a similar range of activity in the final 16 hours of acclimatisation and their experimental phase. This suggests two things.

1. Some atypical locomotor activity may be induced in L. depurator initially, either by stress caused by collection and processing procedures or by reaction to the novel environment of the experimental apparatus. This initial atypical behaviour may take the form of either hyperactivity or total inactivity.

2. A period of eight hours appears to be sufficient for the behaviour of L. depurator to recover from the effects of experimental manipulation.

These results agree with those obtained by Morris (Pers. Comm.) in a study on acclimatisation of the prawn Palaemon elegans. On the basis of these results, the 24 hour acclimatisation period employed in these experiments appears to be more than adequate.

3-4.2 LIGHTING REGIMES

Table 3.6 summarises the results obtained under all three lighting regimes. Two points are immediately obvious.

1. A very clear difference in behaviour patterns exists between crabs collected from the two different types of site. Ten out of twelve (83%) shallow water crabs show cyclic locomotor behaviour while only three out of 22 (14%) deeper water crabs do likewise.

2. Of the ten shallow water crabs which show cyclic behaviour, eight (80%) show a 25 hour cycle with activity peaks corresponding to times of 'expected' night time flood/high tide. No such trend is shown by the deep water crabs. Only three deep water crabs (14%) show cyclic behaviour and in each case a different periodicity is shown. This latter point is further emphasised by Figure 3.36 discussed earlier in which the plateau most likely represents an artefact and not a true periodicity in the time series. This would reduce the percentage of deep water crabs showing rhythmicity to 9%.

One other important point which arises from Tables 3.2, 3.4 and 3.5 is that cyclic locomotor activity is shown by shallow water crabs under each of the three different lighting regimes. This indicates that the cyclic behaviour is not merely a function of a cyclic laboratory environment. Similarly, deep water crabs were shown to be arhythmic under all three lighting regimes.

The answer to the question as to whether L. depurator shows cyclic activity when housed under laboratory conditions (LD 12:12), therefore appears to depend on the site of collection of the crabs. The results show that swimming crabs collected from deep water off the Isle of Cumbrae show patterns of locomotor activity with no apparent cyclic component and equally clearly that crabs collected from shallow sub-littoral sites (3-9 metres) show strong 25 hour cycles of activity.

The deep water animals used in this study were collected from a muddy sediment and from conditions and areas similar to those in

which Nephrops and Goneplax may be found. Both Nephrops and Goneplax have been shown to exhibit clear cut patterns of locomotor activity, apparently entrained by light intensity and quality, with animals leaving their burrows to forage under certain light conditions (Atkinson, 1974; Arechiga and Atkinson, 1975; Oakley, 1978). Although L. depurator is not a burrowing animal, given the other similarities in lifestyles between these animals, one might expect that in deep water, L. depurator might also show some form of cyclic locomotor activity. The results of this study indicate that this is not the case, and there are two possible explanations for the observed difference. L. depurator does not build and live in burrows and it is a highly active crab capable of swimming sideways at a rate of over 1 metre per second with only moderate exertion (Kühl, 1933).

Oakley (1978) suggests that Nephrops emerge from their burrows in response to increasing light levels, forage by sight and return to their burrows to consume any prey items obtained. This may in part contribute to the patterns of activity shown by the prawns. In addition, Nephrops also shows a locomotor rhythm which may be related to burrowing and burrow maintenance activities (Naylor and Atkinson, 1976). L. depurator obviously does not have the latter constraint and also does not return to a given position to consume prey. Field observations reported in Chapter 2 of this thesis indicate that L. depurator, when in possession of a food item may collapse onto or partially sink into the substrate or move quickly to the nearest cover before feeding. Also, being a very effective and agile swimmer, L. depurator may be much more adept at avoiding and escaping from predators than either Nephrops or Goneplax. The flexibility thus gained may enable L. depurator to forage on the

substrate almost continually without the constraint of returning to a home burrow to consume food. In shallow tidal areas, food availability may fluctuate with the state of the tide. In deep waters, it is much more likely that food availability, to L. depurator at least, will remain constant throughout the day. It is therefore possible that with a non-fluctuating food supply, continual foraging, and an ability to avoid predators efficiently, cyclic locomotor behaviour may not be advantageous to L. depurator in deep water.

Crabs collected from two shallow sub-littoral sites however, show very clear patterns of cyclic activity. This behaviour is shown under LD 12:12 conditions, under constant illumination and under constant darkness, suggesting that this is an endogenous rhythmicity. The normal interval between successive high tides is 12.4 hours with 24.8 hours being the standard interval between every other high tide. The results obtained from shallow sub-littoral animals in this study show a clear 25 hour cycle. Visual examination of plots of activity against time also indicate that activity may coincide with periods of 'expected' flood/high tide. The 25 hour cycle may therefore represent the normal 24.8 period between every second high tide. Similar results have been reported for many marine animals (Palmer, 1974).

The two different shallow water sites from which crabs were collected for this study were similar in almost every respect. Both had a sand/mud substrate interspersed with large patches of weed and areas of stones or boulders. In addition, being shallow sites (3-9 metres) both were affected by tidal rise and fall. These tidal considerations were most noticeable at Loch Feochan, currents of up

to 1 knot being common on each flood and ebb tide. The results obtained from the shallow water sites reveal two things; the crabs show strong rhythmic activity patterns and the frequency of these cycles is 25 hours with peaks appearing to coincide with periods of ' expected' night time flood/high tide.

The locomotor behaviour of the shallow water crabs is therefore quite different from that shown by deep water crabs. This difference may in part be explained by the difference in the two environments. Associated with an inflowing tide, there will almost certainly be an influx of both food and of predators. L. depurator may be quite efficient at escaping predation but in high light conditions encountered in shallow water during daylight, the ability to avoid detection must be severely reduced. At the shallow water sites used in this study, a considerable amount of cover was available in the form of weed and rock/boulder slopes, for L. depurator to hide under. This amount of cover was not available at the deep water sites. Therefore, escape from predators at shallow water sites may be achieved in some part by remaining covered during periods of high light intensity, even though food supply may be increased during some of this period. Foraging may then take place during periods of darkness, particularly during periods of increased food supply (flood/ high tide) with a greater chance of predator avoidance.

It is therefore possible to explain the behavioural differences observed between the two types of collection site, in terms of the very different environments encountered. However, a great many other factors may be unaccounted for and more intensive study involving more collection sites is required in order to draw valid

conclusions. No attempt was made during this study to investigate the nature of the underlying clock or control systems of locomotor activity, but work in these fields may also be necessary to understand fully the nature of the activity patterns in L. depurator.

These results have considerable implications for the design of subseq uent experiments. Crabs showing cyclic locomotor activity might also be expected to show different levels of awareness associated with these cycles. This may in turn introduce another variable when studying social interactions in the laboratory, therefore, in light of these findings it was decided to use arhythmic (deep water) crabs in all subsequent experiments in an attempt to reduce the number of possible variables.

3-5 SUMMARY

1. Locomotor activity of 34 individual swimming crabs (L. depurator) was studied in the laboratory using light beams and photoelectric cells to detect activity.

2. Acclimatisation to the experimental apparatus was investigated. A 24 hour acclimatisation period was employed during this study and was chosen in light of the available literature and personal communication (Morris, Taylor). The results of the present study indicate that for L. depurator, a 24 hour acclimatisation period is more than adequate.

3. 3-dimensional plots of activity, time and position in tank were produced as a visual guide to activity patterns produced by individual crabs and as a check on preferential attraction towards areas of the tank. No such preferential attraction which may have affected subsequent analysis was observed.

4. Spectral analysis using autocorrelation and Fourier transformation was employed in order to detect any rhythmicity present in the time-series data.

5. Crabs from two different types of site were studied; a shallow water site (3-9 metres) affected by tidal considerations and with plentiful cover available in terms of rocks and areas of thick kelp; a deep water site (> 30 metres) not affected by tidal

considerations, with an undulating muddy substrate and much less available cover than the shallow water sites.

6. Three different lighting regimes were employed.
   a) Normal laboratory lighting (LD 12:12), 12 hours of light followed by 12 hours of darkness.
   b) Constant darkness (LD 00:24)
   c) Constant illumination (LD 24:00).

7. Significant rhythmicity was displayed under all three lighting regimes, indicating that the activity displayed under LD 12:12 was not induced by the cyclic laboratory environment.

8. Shallow water crabs (83%) displayed significant cyclic locomotor activity while deep water crabs (86%) displayed arhythmic activity.

9. A predominant 25 hour cycle was displayed by shallow water crabs in which peak activity corresponded with 'expected' night time flood/high tide.

10. These results were discussed in relation to the nature of the environment of each of the two types of collection site. It is postulated that the patterns of activity shown by shallow water crabs may be an adaptation to life in a cyclic environment, allowing efficient foraging without a greatly increased risk of predation.

11. The relevance of these findings to the design of subsequent experiments is discussed and it is suggested that arhythmic (deep water) crabs should be used in subsequent laboratory experiments in an attempt to reduce the number of possible variables.

CHAPTER 4

Analysis of the aggressive behaviour

shown by L. depurator during inter-male interactions

in the laboratory.

4-1 INTRODUCTION

Since the time of Darwin, agonistic behaviour has attracted the attention of scientists (Stokes, 1974). The present flow of information on aggression and on its role in sociobiology (Wilson, 1975) reflects a continuing interest in the subject. Both classical ethology and sociobiology have attempted to understand the proximate and the ultimate causes of aggressive behaviour (Brown, 1964, 1969; Stokes, 1974; Wilson, 1975; Maynard-Smith and Parker, 1976; Verner, 1977) with most studies concentrating on vertebrates, especially their territorial systems. Attention has also focused on the apparent frequency with which conflicts are settled without damage to the contestants and the evolution of fighting techniques which minimise the risk of injury.

Most fighting occurs over limiting resources and comparative studies indicate that a minimum of three pre-requisites is necessary for aggression to occur to a significant degree (Dingle, 1983). First there must be a resource worth defending (Brown, 1964; McArthur, 1972) such as food, space, shelter, mates or some combination of these. Second, there must be the ability to defend the resource (Parker, 1974). This usually involves some combination of behaviourial and morphological traits, the latter including increased body size or the development of effective weapons. Third, the source must be defendable. Scattered resources may lead to an ineffective defence because they are too diffuse or too costly. Within the constraints imposed by these prerequisites, there is nevertheless extensive variation among animals in both the occurrence and the precise form

of aggression, requiring explanation in both motiviational and functional terms.

Based on Dingle's (1983) criteria, crustaceans offer several advantages for the study of aggressive behaviour. Many species in several orders clearly possess resource holding potential in the form of chelae, claws and spines that make them formidable opponents in combat (Dingle, 1983). In some instances, as is the case with hermit crabs, the value of the resource (mollusc shells) in terms of its abundance or preference can be precisely determined (Scully, 1983). Because of their intermediate size, many species are large enough to be observed readily in the field and small enough to be maintained in the laboratory, allowing comparison to be made in the testing of hypotheses. Finally, the high level of activity of these animals allow the collection of large amounts of data from relatively short interactions, an important consideration in quantifying behaviour. Crustaceans are therefore amenable to intensive study of behaviour and this has been carried out for a range of species, raising the possibility of comparative methods between both populations and species.

There is extensive literature describing the aggressive behaviour of numerous crustaceans. Hyatt, (1983) reviewed the field and summarised data representing some 20 genera. Most of the studies involved description of aggressive postures and their sequential relationship, analysis of inter- and intra-specific dominance relationships, and speculation regarding the adaptive significance of aggression within the framework of ecological demands made of the combatants. Reviews by Salmon and Astaides (1968), Frings and

Frings, (1968), Crane, (1975), Warner, (1977) and Weygold, (1977) also deal with crustacean aggression and communication to some extent. The decapods in particular have received attention from ethologists and ecologists specifically interested in aspects of the aggressive interactions within species; again territoriality, dominance and individual distance/recognition are the main topics of study. Many investigations have been qualitative and anecdotal, but some have been detailed quantitative analyses of information transfer during agonistic interaction while others have dealt with the study of factors which influence the course and outcome of fights.

The most obvious variable likely to influence fighting ability is body size but prior ownership of a resource may also be important. Large animals of the same species are very likely to defeat smaller animals of the same species and usually also of different species, provided there are no obvious differences in weapons (Dingle, 1983). When groups of 3 or 4 crayfish, Procambarus alleni were placed together in an aquarium (Bovbjerg, 1956), they formed a linear dominance order with larger individuals displacing smaller ones from shelter. In fiddler crabs (Uca pugilator and U. pugnax), wanderers move over the beach and fight for burrows with the residents which constructed them. Almost invariably, when a wanderer suceeds in sucessfully evicting a resident from a burrow, it is the larger of the two contesting grabs (Hyatt and Salmon, 1978). Studies on hermit crabs (Hazlett, 1978), snapping shrimps (Schein, 1975), and stomatopods (Dingle and Caldwell, 1969; Caldwell and Dingle, 1979) also clearly indicate that the larger combatant has an advantage in fights. In this respect, hermit crabs are interesting because their apparent size is a function not only of actual size, but also of the size of the gastropod

shell they occupy. Hazlett (1970) showed that by increasing the visual size of a hermit crabs shell, they also significantly increased the chances of an opponent retreating during an encounter. Increasing the weight of the shell increased the aggressiveness of the occupant crab which were more likely to initiate and win shell fights. If the apparent size of one crab was increased relative to another it also tended to dominate aggressive interactions (Hazlett, 1966a) again suggesting the importance of apparent size.

In many interactions, an approach by one animal may be sufficient to elicit retreat by the other. If retreat is not elicited then signals may be exchanged. The raising of one or more legs is common and in the frontal approach commonly used by hermit crabs and spider crabs a pair of legs may be raised together to produce a distinctive cross shaped posture (Hazlett, 1972b, 1972c). Hazlett, (1972c) by studying the reaction of hermit crabs to models also showed that such a posture elicits retreat in an opponent and could be made more effective by increasing the length of the models' outstretched legs. In live hermit crabs, leg length correlates with body size and in natural double leg raises it may be size that is being signalled.

Cheliped presentations are also common in decapod fights and in some instances appear to be used only after leg raise postures. In the blue crab Callinectes (Jackowski, 1974) and for the hermit crab Pagurus (Hazlett, 1966a) the lowest intensity chelae posture is to hold the chelipeds tightly against the front of the body. This is often combined with a low body position (decreasing apparent size) and with retreat. Most other chelae postures also appear to influence the behaviour of opponents and in particular to elicit retreat. This

justifies the use of the term threat display for this type of behaviour. Chela presentation in hermit crabs involves bringing the chelipeds forward into a position in which the outer faces are displayed, the tips pointing directly down (Hazlett, 1966a). Threat is increased by chela extension in which the chelipeds are moved from presentation into a horizontal position with the tips pointing forwards.

In brachyuran crabs, two very common cheliped postures are shown. In the first, the chelae are moved out from the body such that the opened fingers of the claw point forwards, while in the second the chelipeds are raised up and spread as widely as possible in a full meral display. Warner (1977) suggests that these represent two distinct levels of threat, the latter being more intense presumably because it is more likely to elicit retreat.

The exchange of agonistic signals and associated advances or retreats is usually sufficient to resolve an encounter, implying that fights may involve assessment of one individual by another. However, in some cases such as evenly matched pairs, fights may escalate to physical violence. Goniopsis push against each other using the outer faces of the chelipeds in a shield position and Aratus pushes against an opponent with interlocked chelae in the outstretched position (Warner, 1970). The Italian river crab Potamon fluviatile (Vannini and Sardini, 1971) uses both pushing and grasping, and striking with the tips of the chelae is seen in Potamon, Callinectes (Jackowski, 1974) and Goniopsis (Warner, 1970). In most cases, however, injury to either contestant is rare.

The selective forces moulding aggressive interactions among animals may be analysed using a theoretical approach based on games theory (Maynard-Smith and Price, 1973; Maynard-Smith, 1974, 1976 & 1982; Parker, 1974; Maynard-Smith and Parker, 1976; Caryl, 1979). In the context of fighting, the games theory approach specifies a set of possible patterns of behaviour or strategies and the harmful and beneficial effects derived in a fight by animals using each strategy against opponents using all possible strategies. Knowing the frequency of the strategies in a population and therefore the probability of each kind of fight, the overall pay-off (or fitness) of each phenotype can be calculated. It is then possible to assess which strategies will increase in frequency over successive generations and in particular whether any is an evolutionary stable strategy (ESS), i.e., when most members of a population use the strategy, it cannot be bettered by any other member of the defined strategy set.

The Hawk-Dove model and the War of Attrition were the first two games theoretical analyses of aggression and these have been discussed exhaustively. The main insight of these two models are that conventional fighting and escalated fighting are likely to co-exist, that animals are unlikely to give deliberately any information about their intentions and that giving up should occur unpredictably (Maynard-Smith, 1982). These two models are based on a highly simplified view of animal fighting. In particular, they assume that all animals are identical except in their behaviour. For this reason, Maynard-Smith and Parker (1976) developed a series of models involving asymmetry. In the case of an uncorrelated asymmetry, what an animal does depends on arbitrary considerations such as who arrived first. Other asymmetry may also exist with respect to the

value of the resource or the fighting ability or resource holding potential (RHP). On this last point, several models show that animals which are able to assess reliably their own RHP relative to that of their opponent, and make decisions about whether, and how to fight, on this basis will do better than those who ignore this asymmetry. In addition, especially where relative RHP is small it may not be possible to assess the relative RHP at the start of fight and several models (Maynard-Smith and Parker, 1976; Parker and Rubenstein, 1978) have analysed fights as a process of gradual acquisition of information about relative RHP. The general predictions are that fights are likely to be longer and more intense when animals are evenly matched.

Re-analysis of some ethological data (Caryl, 1979) fitted surprisingly well the predictions of the War of Attrition model. In some species the distribution of fight lengths was a negative exponential and while some displays were reliably followed by escape, none allowed clear prediction as to whether an animal would attack. In the light of this and other analyses the concept of a display as used in classical ethology has been reconsidered.

Perhaps the most important point arising from all the discussion about games theory is not that one particular model is the most successful in accounting for the form of animal fighting, but that development of such models should stimulate ethologists to examine their data and assumptions in a new light. The games theory approach to animal fighting has received a great deal of attention from both theoretical and practical biologists and this way of looking at the adaptive significance of aggression has clarified a number of

complex theoretical issues and has stimulated empirical research (Huntingford, 1984). In this respect, some scientists studying the fighting behaviour of crustacea have been particularly receptive, including Hyatt (1983) on the effects of size and prior ownership of burrows on outcome of interactions and Hazlett (1972b, 1972c) on the effects of size and shell resource value on initiation and levels of escalation in hermit crab fights.

As discussed previously, the crustaceans lend themselves to the study of aggression and the sequencing of behaviour. While a great many studies of this type have been undertaken, the Portunidae, as a group, have received surprisingly little attention. L. depurator has been shown to be an aggressive animal in the field and in the laboratory. In addition, the flattened dactylus (swimming paddle) of the fifth pereiopod has a conspicuous central spot surrounded by a vivid blue band. These markings are very prominent under natural conditions and particularly so when the swimming legs are held above the carapace as is characteristic during aggressive interactions. These behaviour patterns shown during initial casual observation are of considerable theoretical interest and as discussed before (see Chapter 1), L. depurator lends itself as a starting point for any cross species comparison within the Portunidae. The present study was designed with the following objectives.

1. To characterise the movements and postures and the normal course of events in a fight between male crabs; to relate this to the behaviour patterns shown in the field studies (Chapter 2) and to make some deductions concerning the mechanisms controlling the behaviour.

2. To investigate the possibility that consistent individual differences in the style of aggressive behaviour exist.

3. To investigate the effect of size on the initiation, form and outcome of interactions.

4. To investigate the behavioural differences shown between winning crabs and losing crabs.

4-2 MATERIALS AND METHODS

4-2.1 COLLECTION AND PROCESSING OF ANIMALS

Results obtained from Chapter 3 of this thesis indicated that L. depurator from sites affected by tides, exhibited cyclic locomotor activity. Associated with any such rhythm must be a fluctuating responsiveness which may affect much of the other behaviour of the animal. In order to remove this possible source of error, it was decided to use crabs which showed no rhythmic locomotor activity. Crabs collected from deep water off Millport, Isle of Cumbrae did not exhibit rhythmicity (Chapter 3) and for this reason, crabs from this site were employed in this section.

Crabs were collected by dredge from the Firth of Clyde (Figure 2.1) and transported to Glasgow by rail. On arrival in Glasgow each crab was measured (carapace width, mm) and its physical condition assessed. Crabs with missing limbs or heavy covering of encrusting organisms were classified as unfit animals and discarded, as were crabs in immediate post-moult condition (see Chapter 2). The soft cuticle of these post-moult crabs would make them easy prey for other crabs. In addition, Hazlett (1966) in a study on Diogenid hermit crabs, showed that recently moulted crabs were readily attacked and more easily lost shell fights than crabs in intermoult condition.

It is possible that the possession of eggs by a female crab may modify its behaviour, particularly in its reactions to other crabs. Similarly, the behaviour of a female crab may be modified on transition from

non-copulatory to copulatory condition. In the latter, the behaviour of accompanying male crabs would undoubtedly also be modified. For these reasons, only male crabs were employed in this study.

Each crab was marked with an individual identification number embossed on dymo tape. These numbers were attached to the intestinal region of the carapace (Figure 4.1) using quick drying dental cement. This marking technique was used for the following reasons:-

1. The numbers were small and light thereby causing little inconvenience or disturbance to the crabs.
2. Numbers on the intestinal region would not be visible to another crab during an interaction and could not therefore influence in any way the outcome of the interaction.
3. Marks of this form were easily visible on video-tape recordings of the interactions, facilitating recognition of individual crabs.

Claw tags such as those used in the study of the ecology and behaviour of L. depurator in the field (Chapter 2) were deemed to be unsuitable in the current investigation, as any addition to the chelipeds, particularly of a coloured nature would be visible to another crab and may therefore influence the outcome of an interaction.

4-2.2 EXPERIMENTAL PROTOCOL

After marking, the crabs were transferred to individual glass tanks (60 x 38 x 30 cms) and fed 2 gms of M. edulis in an attempt to

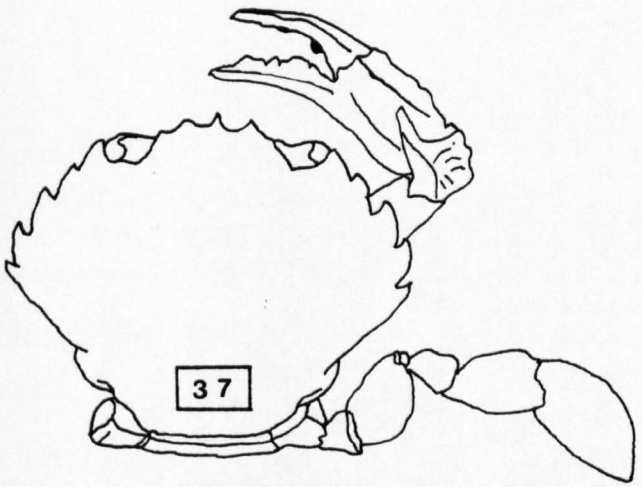


Figure 4.1 Showing position of individual identification number on posterior region of the carapace.

standardise hunger which may have some influence on aggressiveness. After 24 hours any uneaten food was removed and the crabs left for a further 24 hours. Results of the acclimatisation investigation (3-2.5) indicate that 24 hours is more than adequate to allow L. depurator to recover from stress induced by experimental manipulation.

Each glass tank was identical in every respect, filled with sea water to a depth of 30 cms on a 3 cm layer of sand and mud and connected to a circulating sea water system (3-2). Black blinds surrounded each tank on 3 sides with an opaque perspex shield covering the fourth. In this way, animals were totally isolated from external disturbance. A small observation port (6 x 4 cm) in the perspex shield allowed observation and filming to be carried out without disturbance to the animals. Throughout this study, animals were maintained under a standard 12:12 LD lighting regime. Illumination was provided by fluorescent tube balanced for daylight and transition of light state was abrupt. No attempt was made to mimic the natural photic environment of the crabs.

After acclimatisation, two crabs were removed from their individual holding tanks and placed at opposite ends of an identical experimental tank. This use of a separate experimental tank was an attempt to remove any possible home tank bias which may have affected the outcome of an aggressive encounter as is known to occur with the intertidal burrowing crab Uca (Griffin, 1968). Some stress was inevitably induced by this transfer procedure, but this should be similar for both crabs and it was felt that the overall effects of this would be much less than that of possible home tank bias. Prior to transfer of crabs, 3 ml of liquidised M. edulis was added to the

experimental tank. This was designed to induce locomotor activity and thereby bring the crabs in to contact.

Immediately on placement of the crabs into the experimental tank, video-tape recording commenced. A Schibaden video camera was used with a wide angle lens giving good definition over the whole tank. No special lighting was required. Recording was continued from introduction of the animals until the first interaction of the crabs was deemed to have finished. For the purpose of this study, an interaction was defined as having commenced when one of the crabs orientated or moved towards the other, and having terminated on collapse of one crab onto the substrate or by retreat of one individual from a stationary opponent. After filming, the crabs were returned to their home tanks and another pair of crabs transferred to the experimental tank. For logistical reasons, experimental groups were restricted to a maximum of six crabs and within each group, each individual crab was paired with every other as far as possible, in a round-robin series of interactions. Some of the groups however remain incomplete due to death of one or more individuals while in isolation tanks.

Certain pairs of crabs were placed together on more than one occasion in an attempt to investigate the possibility that consistent individual differences in style of aggressive behaviour existed. As discussed previously (Chapter 3), Hazlett (1966) has shown that the results of aggressive encounters in the immediate past of an individual hermit crab can affect its behaviour in the present. In order to counteract any such effects in this study, each crab was returned to its home tank after a filming bout and isolated for at

least 48 hours before being paired in another interaction. Each crab was fed 2 gm of M. edulis on return to its home tank. On completion of a full series of interactions, crabs were returned to a large holding tank and a new group of male crabs collected.

Eight separate groups of animals were employed and the size of each individual (carapace width, mm) within each group is shown on Table 4.1 while Table 4.2 shows the paired interactions which were recorded. 107 interactions were recorded from the eight different groups and 44 individual crabs were used. A size difference index (see P 107) (SDI) was calculated for each pair of interactiong crabs (Figure 4.2). SDI ranged from 0.02 - 0.67 with a mean value of 0.19 and standard deviation of 0.16.

After filming, a digital time clock display (showing elapsed time to 1/100 second) was superimposed onto the tape. This time display allowed accurate assessment of the elapsed time within an interaction and allowed each interaction to be investigated at a frame by frame level. For the purposes of this study, a frame was defined as 0.5 second, a sampling rate which allowed a detailed study of the behaviour patterns to be made. At each frame, the body and limb positions of each of the interactants was observed and recorded, thus providing a complete record of events throughout each interaction. In addition to these paired interactions, a number of single animals were filmed in the experimental tank as a control. Filming commenced from point of introduction to the experimental tank and lasted for 50 frames, a period equivalent to the average interaction length recorded during paired crab interactions (see 4-3). Exactly the same parameters were measured for a single crab as for

	Group Number							
	1	2	3	4	5	6	7	8
Size of Crabs (Carapace width, mm)	52	45	52	46	48	50	53	55
	45	43	45	35	46	48	45	46
	31	31	50	50	41	44	44	44
	43	52	48	36	43	51	48	50
	41	41	41	51	37	54	49	41
	47	-	33	48	-	-	40	-
	—	—	—	—	—	—	—	—
n =	6	5	6	6	5	5	6	5
Range	31-52	31-52	33-52	35-51	37-48	44-51	40-53	41-55

Table 4.1: Showing distribution of crab size in the eight experimental groups.

Group A

Crab size (mm)	52	47	45	43	41	31
52	-	1	1	1	1	1
47		-	1	0	1	1
45			-	0	0	0
43				-	1	1
41					-	2
31						-

Group B

	52	45	43	41	31
52	-	2	1	1	2
45		-	1	2	1
43			-	0	2
41				-	3
31					-

Group C

	52	50	48	45	41	33
52	-	3	3	1	1	1
50		-	2	1	1	1
48			-	1	1	1
45				-	1	1
41					-	1
33						-

Group D

	51	50	48	46	36	35
51	-	2	1	1	1	1
50		-	1	1	1	1
48			-	2	1	1
46				-	1	2
36					-	2
35						-

Group E

	48	46	43	41	37
48	-	1	1	1	0
46		-	1	1	1
43			-	1	1
41				-	1
37					-

Group F

	54	51	50	48	44
54	-	1	1	1	1
51		-	1	1	1
50			-	1	1
48				-	1
44					-

Group G

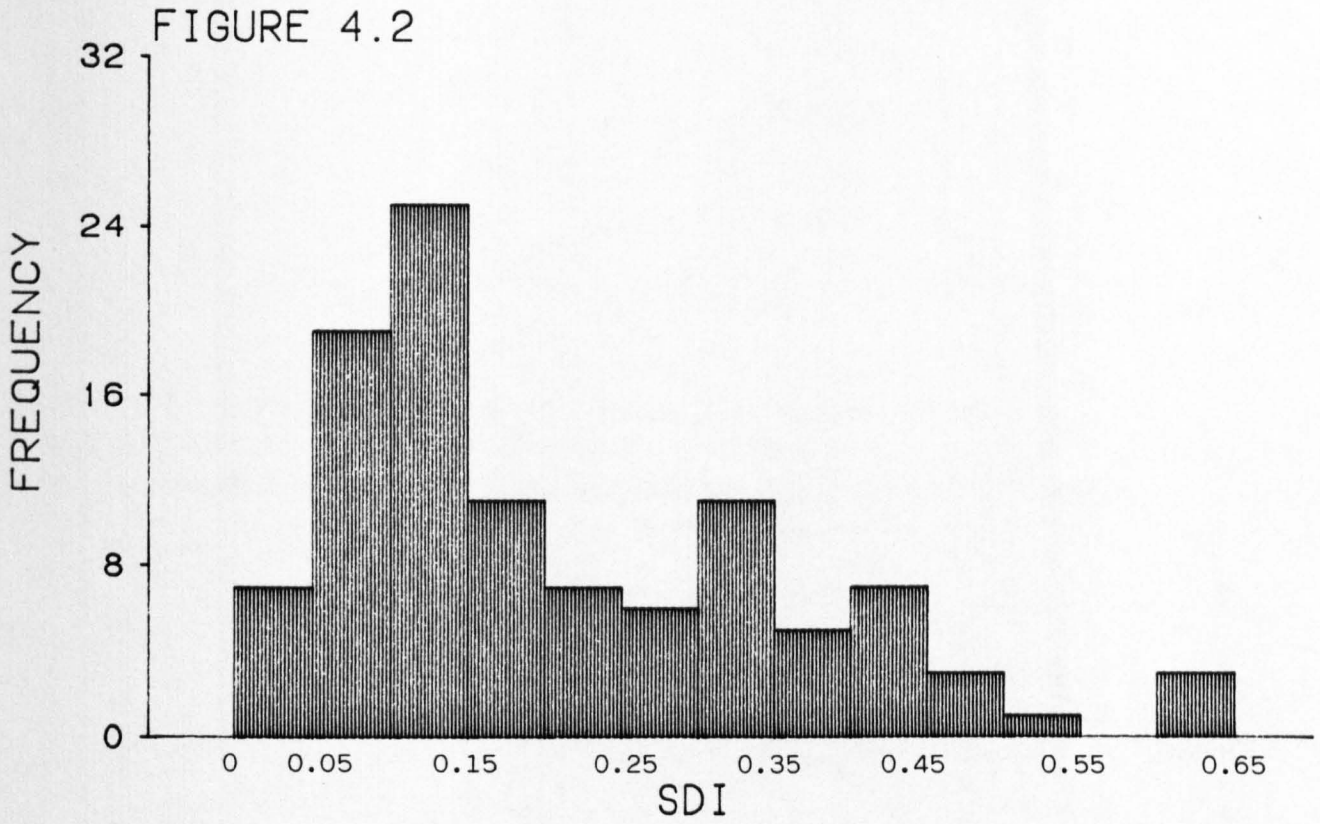
	53	49	48	45	44	40
53	-	1	1	1	1	1
49		-	1	1	1	1
48			-	0	0	0
45				-	1	1
44					-	1
40						-

Group H

	55	50	46	44	41
55	-	1	1	1	1
50		-	1	1	1
46			-	1	1
44				-	1
41					-

Table 4.2: Showing distribution of interactions recorded from each experimental group. Values in matrices indicate the number of interactions between the individuals concerned.

FIGURE 4.2 RANGE OF SIZE DIFFERENCES



each crab in a paired interaction. The size range of the single crabs (33 mm - 54 mm, $\bar{x}$ = 42, n = 5) was equivalent to the size range of crabs in paired encounters (31 mm - 55 mm, $\bar{x}$ = 45, n, = 44).

4-2.3 FRAME BY FRAME ANALYSIS

Extensive preliminary observations of group interactions and the available literature on agonistic behaviour in crustacea (for review see Hazlett, 1972), suggested that the factors most likely to influence an interactant are; body position and height; position of chelipeds; form and speed of approach; and in the case of L. depurator, position of swimming legs. During interactions with conspecifics and potential predators (see 2-3.5) the swimming legs are held above and often waved backwards and forwards over the carapace. These movements are similar to, but much slower than the movements which occur during swimming behaviour, and it is possible that they may have some significance during an interaction. For this reason, particular attention was paid to the position and movements of the swimming legs.

For each crab, the following information was obtained for each frame (0.5 second) during an interaction by stopping the video tape (accurate to 1/100 second) and observing the position of each animal. The information was recorded on computer coding sheets and transferred to computer file for storage and analysis.

Parameters recorded at a frame by frame level, for each crab.

1. Frame number
2. Body angle
3. Body height
4. Status of left swimming leg (fifth pereiopod)
    a) Angle in medial plane
    b) Angle in saggital plane
    c) Extension
    d) Paddle angle
5. Status of right swimming leg (fifth pereiopod)
    a) Angle in medial plane
    b) Angle in saggital plane
    c) Extention
    d) Paddle angle
6. Status of left cheliped
    a) Angle in horizontal plane
    b) Angle in vertical plane
    c) Status of chela.
7. Status of right cheliped
    a) Angle in horizontal plane
    b) Angle in vertical plane
    c) Status of chela
8. Locomotion type.
9. Direction of locomotion relative to opponent.
10. Orientation in relation to opponent.
11. Distance from opponent.
12. Position of crab in relation to opponent.
13. Strike other crab.
14. Grasp other crab.
15. Interaction identification.

Description of parameters

1. Frame number

   An interaction was defined as having commenced when one crab moved in a deliberate manner or orientated towards its opponent. The videotape was stopped when this was deemed to have occurred and the time noted. Although the time clock was accurate to 1/100 second, the start time was noted to the nearest 1/10 second and this was taken as frame 1. The videotape was then advanced in 0.5 second intervals and the above parameters measured for each frame. The frame number was therefore an indication of the elapsed 0.5 second intervals during an interaction.

2. Body angle

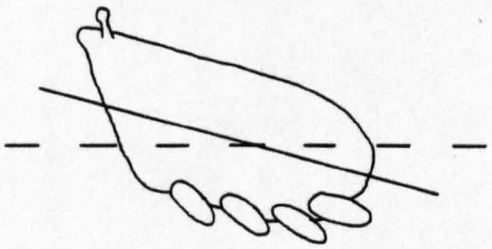
   Body angle was scored as being horizontal, slightly tilted, or fully tilted (Figure 4.3). When an imaginary line drawn through the centre of the body in an antero-posterior direction was 45° or more to the horizontal, the body was defined as being fully tilted. When this imaginary line was horizontal to the substrate, the body was defined as horizontal. Any position between these two extremes was defined as slightly tilted.

3. Body height

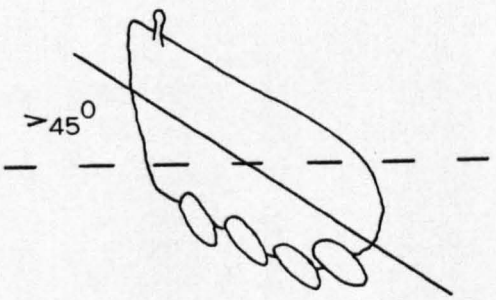
   Body height was scored as being collapsed, partially raised or fully raised (Figure 4.4). If the ventral surface of the crabs body was pressed against the substrate or pressed into the substrate, it was scored as being collapsed. If the body was not in contact with the substrate and the ambulatory legs not extended, it was

Figure 4.3 Body angle

Horizontal



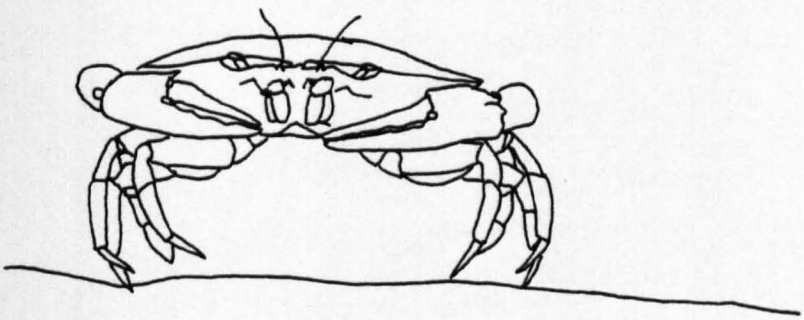
Slightly tilted



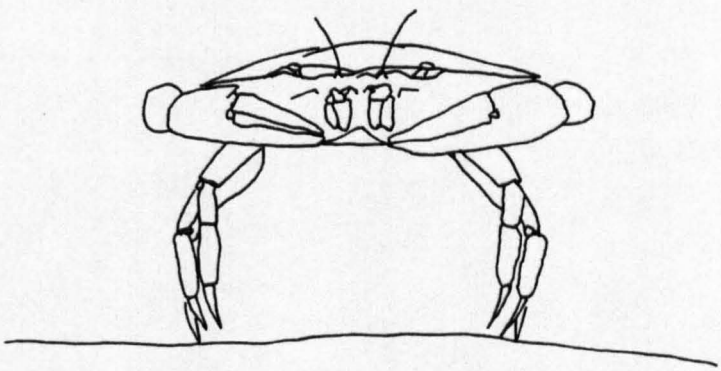
Fully tilted

Figure 4.4 Body height

Collapsed



Partially raised



Fully raised

scored as being partially raised. Fully raised was scored if the body was not in contact with the substrate and the ambulatory legs fully extended, thereby raising the body to its maximum height.

4. & 5. Status of swimming legs

a) Angle in medial plane

A swimming leg was scored as being up, level or down if the mid-point of the dactylus or paddle was above, level with, or below the posterior carapace margin (Figure 4.5).

b) Angle in saggital plane.

A swimming leg was scored as forward, level or back if the dactylus was anterior, level with, or posterior to the posterior carapace margin (Figure 4.6).

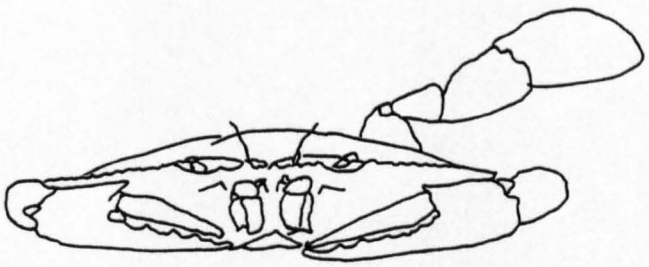
c) Extension

A swimming leg was scored either as extended or not extended (Figure 4.7). Extension refers to all segments of the limb except the dactylus, and if a straight line could be drawn through all segments of the limb from the coxa to the propodus, the limb was defined as extended. Any other position of the limb was defined as not extended.

d) Paddle angle

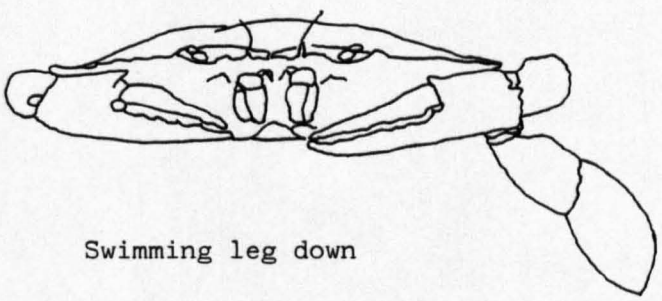
Paddle angle was scored as either bent or straight and refers to the angle between the propodus and the dactylus or paddle of the limb (Figure 4.8). If a straight line could be drawn through the limb from the tip of the dactylus to the mid point of the propodal-carpal line, the paddle angle was classed as straight. Any other position was classed as bent.

Figure 4.5 Status of swimming leg in medial plane



Swimming leg up

Swimming leg level



Swimming leg down

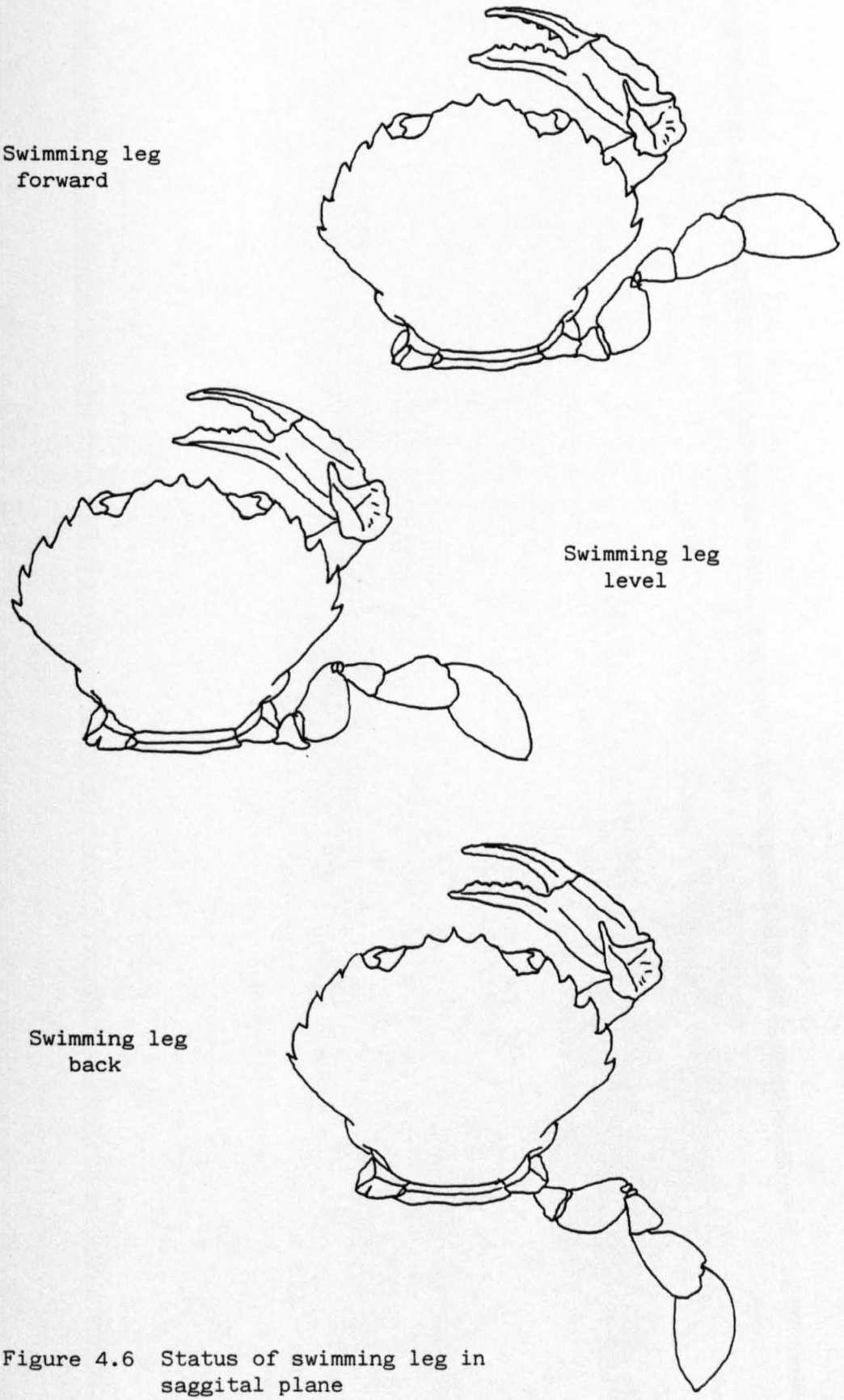
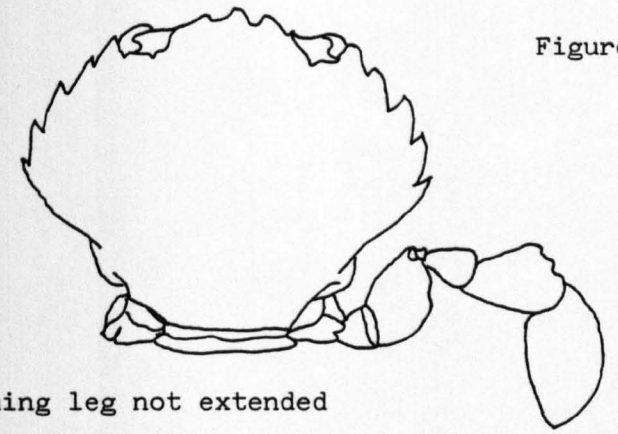
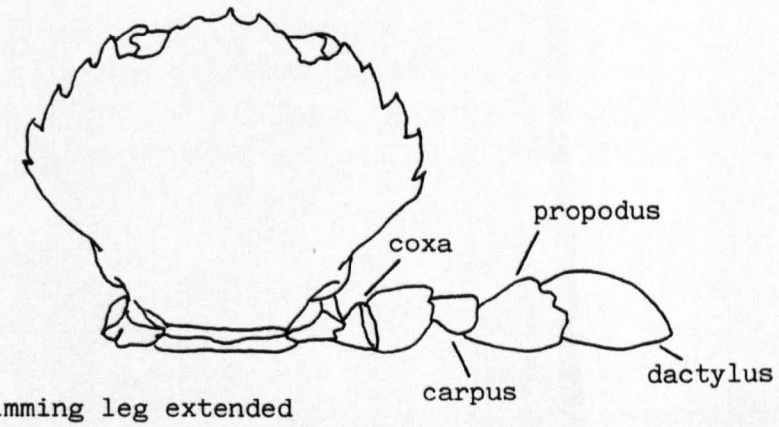


Figure 4.6 Status of swimming leg in saggital plane

Figure 4.7 Swimming leg extension

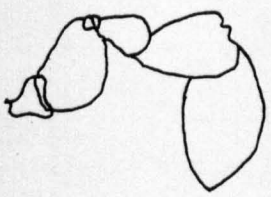


Swimming leg not extended



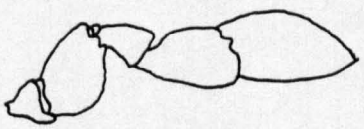
Swimming leg extended

Figure 4.8 Swimming leg paddle angle



Swimming leg bent

Swimming leg straight



Points a)-d) above were scored and recorded independently for both the left and right swimming legs.

6. & 7. Status of chelipeds.

a) Angle in horizontal plane

A cheliped was scored as being folded, out or extended (Figure 4.9). If the inner face of the propodus of the cheliped was held against the antero-lateral carapace margin, the cheliped was defined as being folded. If a straight line could be drawn from the tip of the dactylus through the mid-point of the carpal-propodal line to the base of the limb, the cheliped was defined as extended. Any position where the cheliped was neither folded nor extended, was defined as out.

b) Angle in vertical plane

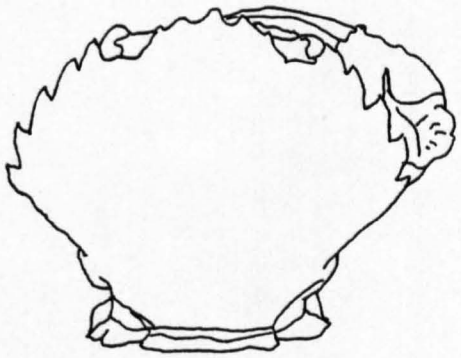
A cheliped was scored as being either level or down (Figure 4.10). If the cheliped was held parallel to a line drawn from the mid posterior carapace margin to the mid anterior carapace margin, the cheliped was classed as being level. Any other position was classed as down.

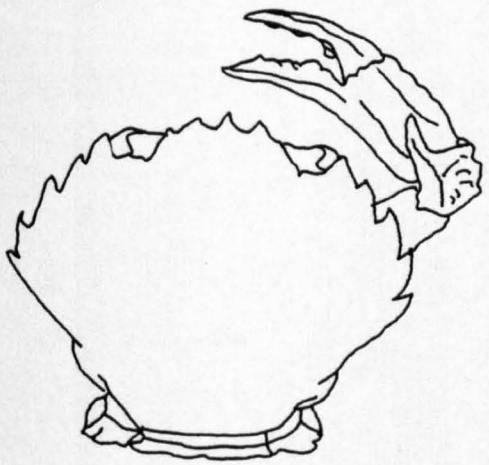
c) Status of chela

This was scored as being either open or closed. If the dactylus of the chela was in contact with the propodal process, the chela was closed. If there was no contact, the chela was defined as open.

Points a)-c) above were scored and recorded independently for both the left and right chelipeds.

Cheliped folded





Cheliped out

Cheliped extended

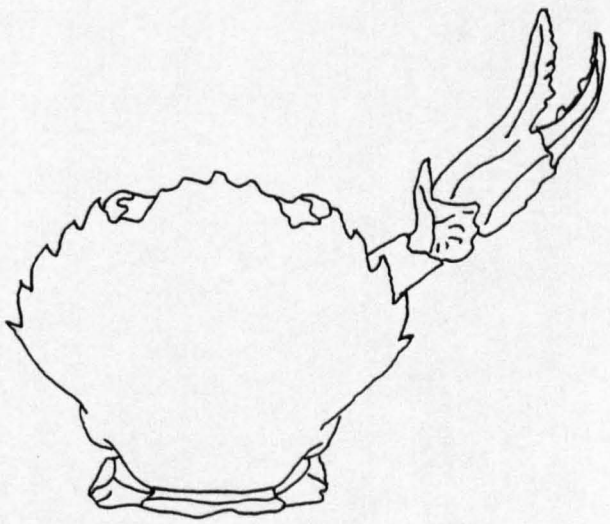
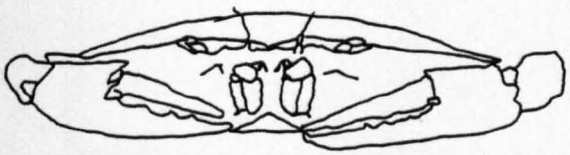


Figure 4.9 Status of chelipeds in horizontal plane



Chelipeds level

Chelipeds down

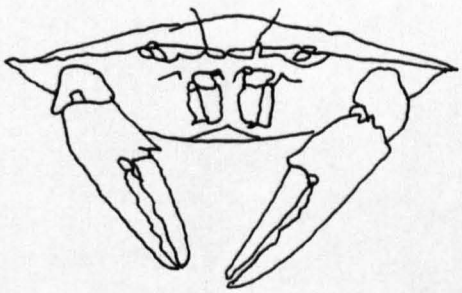


Figure 4.10 Status of chelipeds in vertical plane

8. Locomotion type

This was scored as slow walking, fast walking, swimming or stationary. Slow walking was defined arbitrarily as less than one body length per frame while fast walking was defined as greater than one body length per frame.

It is not possible to detect locomotion type by viewing a still video frame. Therefore, in order to obtain this information, each interaction was viewed at normal speed and the real time of occurrence and length of locomotion types was noted for each crab. It was then possible, by looking at the real time of each sampling point (frame), to determine the locomotion type of the crabs at that point.

9. Direction of locomotion relative to opponent.

This was defined as approaching opponent (by any of the locomotion types described in 8) above), retreating from opponent, or remaining stationary. As with locomotion type, it is not possible to detect whether an animal is approaching or retreating, by viewing a still video frame. The same technique was therefore applied to this as described in 8) above.

10. Orientation in relation to opponent. This was scored as either facing opponent or not facing. Any position where the antero-lateral carapace margins of the two crabs were not parallel was taken as not facing.

11. Distance from opponent

This was an estimate of distance between two crabs in terms of body length.

12. Position of crab in relation to opponent

This was scored as level, on ground, or in mid-water. If both crabs were in contact with the substrate they were classed as being level. Similarly, if both crabs were in mid-water they were classed as level. However, if one crab was on the substrate and the other in mid-water, the non-swimming crab was defined as on ground and the other as mid-water.

13. Strike other crab

If a crab was in the act of striking the other with any part of its body, this was recorded.

14. Grasp other crab.

If a crab was in the process of grasping any part of the other with either of its chelipeds, this was noted.

15. Interaction identification.

For each interaction, the group identification (Table 4.1), the size and individual identification of the two interactants and the position on the video-tape were recorded. In addition, the identity of the initiator and winner of each interaction was noted.

If any of the above parameters were not evident due to parts of the body of one crab being obscured by the other, these were scored as missing values and the computer programs used in the analysis were equiped to take this into account. The missing value code was rarely used.

Subsequent to the above information from each interaction being transferred to computer file, each dataset was scanned and a number of different patterns of limb and body position were identified from the original raw variables. This scanning was carried out by a computer programmed to identify raw variables (parameters) and to note when pre-defined groups of these parameters occurred together. These groups of parameters (patterns) were predefined on the basis of extensive preliminary observation of interaction between crabs which allowed regularly occuring patterns to be identified. Scanning by computer was carried out for each frame, and a body and limb pattern for each crab was identified and stored.

The most obvious variable likely to influence fighting ability is body size (Dingle, 1983) and Hazlett (1970) has shown that in the hermit crab, Clibanarius vittatus, increasing the visual size of an animals shell significantly increased the chances of an opponent retreating during an encounter. Visual size, therefore, seems to be an important factor in crustacean aggression and for this reason the patterns of limb and body position identified in the aggressive interactions between L. depurator are ranked according to visual size presented to an opponent. Pattern 1 (below) presents the largest frontal area to an opponent while Pattern 13 presents the smallest. The patterns of limb and body position which were identified are as follows.

Pattern 1

Body fully tilted and fully raised off the substrate. Chelipeds extended and level, with chelae open. Swimming legs above posterior carapace margin, extended and paddle angle straight (Figure 4.11).

Pattern 2

As for Pattern 1, but paddle angle bent as opposed to straight (Figure 4.12).

Pattern 3

Body fully tilted and fully raised off the substrate. Chelipeds extended, level, and chelae open. Swimming legs level with the posterior carapace margin, extended and paddle angle straight (Figure 4.13).

Pattern 4

Body slightly tilted and partially raised off the substrate. Chelipeds extended, level and chelae open. Swimming legs above posterior carapace margin, extended and paddle angle straight (Figure 4.14).

Pattern 5

As for Pattern 4 but paddle angle bent as opposed to straight.

Pattern 6

Body only slightly tilted and partially raised from the substrate. Chelipeds extended, level and chelae open. Swimming legs level with posterior carapace margin, not extended and paddle angle bent. (Figure 4.15)

Pattern 7

Body fully tilted and fully raised above the substrate. Chelipeds down, chelae open. Swimming legs above posterior carapace margin, extended and paddle angle bent. (Figure 4.16)

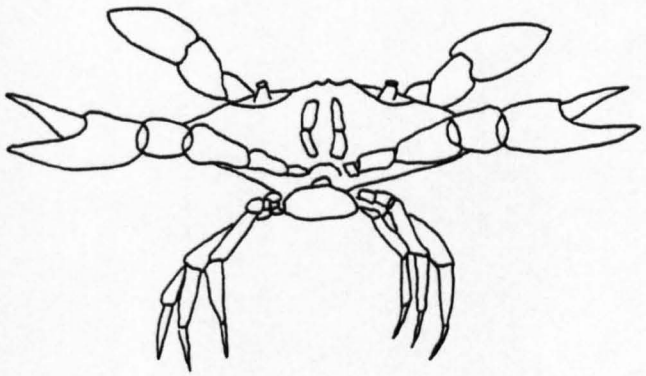


Figure 4.11 Pattern 1

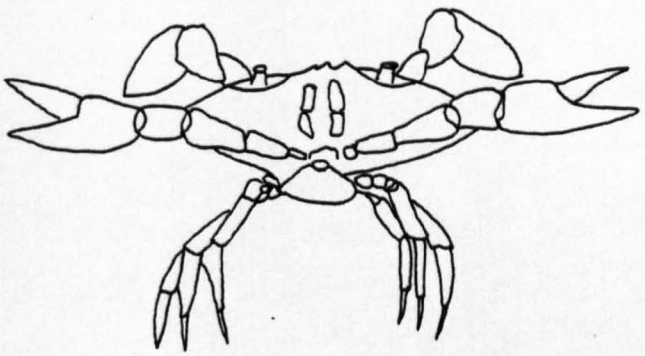


Figure 4.12 Pattern 2

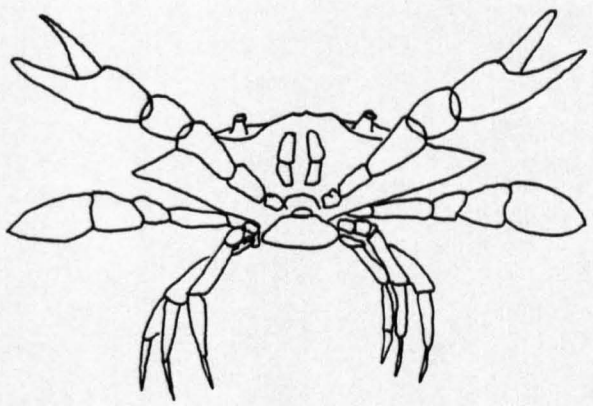
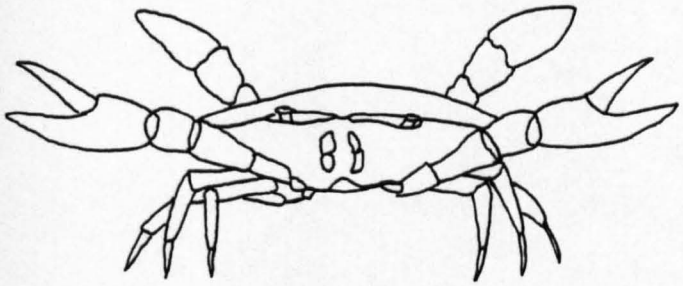


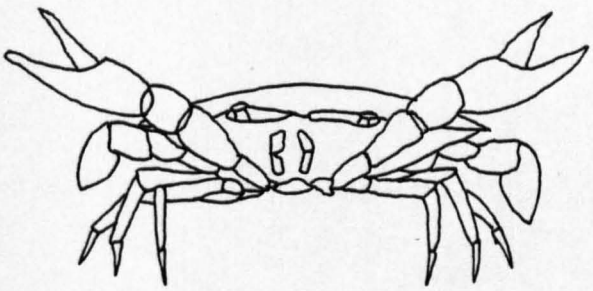
Figure 4.13 Pattern 3

Figure 4.14



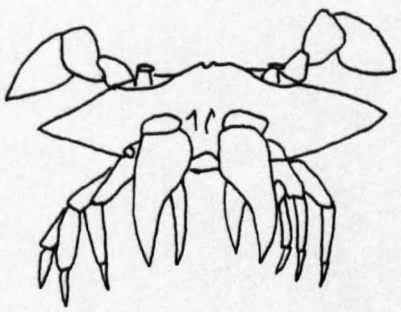
Pattern 4

Figure 4.15



Pattern 6

Figure 4.16



Pattern 7

Pattern 8

As for Pattern 7 but swimming legs not raised above posterior carapace margin and not extended. (Figure 4.17)

Pattern 9

As for Pattern 7 but body not fully tilted and not fully raised above substrate. (Figure 4.18)

Pattern 10

Body slightly tilted and partially raised above the substrate. Chelipeds down. Swimming legs not raised or extended. (Figure 4.19)

Pattern 11

Body slightly tilted and partially raised off the substrate. Chelipeds folded. Swimming legs not raised or extended (Figure 4.20).

Pattern 13

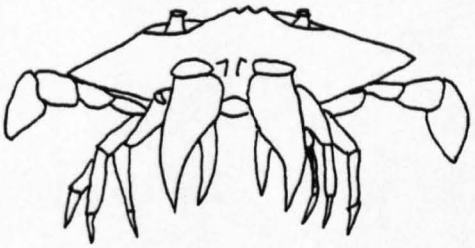
Body collapsed onto the substrate. Chelipeds and all other limbs folded into the body (Figure 4.21).

The above represent the different limb and body patterns observed during aggressive interactions. A further nine factors were identified and although not strictly patterns in the sense used above, they are recorded as patterns for the sake of convenience.

Pattern 12

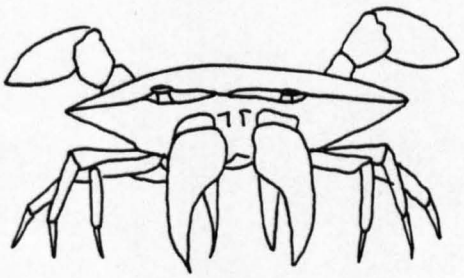
Feeding movement. This signified movement of one or both chelipeds from the substrate (down position, Figure 4.10) to the mouthparts (folded position, Figure 4.9). No account was taken of transfer of particulate matter to the mouthparts, only of movement of the limbs.

Figure 4.17



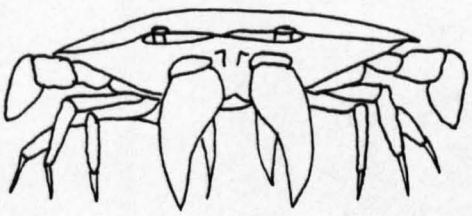
Pattern 8

Figure 4.18



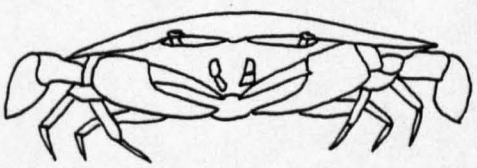
Pattern 9

Figure 4.19



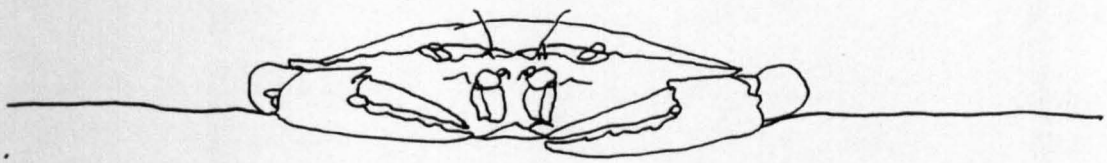
Pattern 10

Figure 4.20



Pattern 11

Figure 4.21



Body collapsed onto the substrate

Pattern 14

Swimming leg movement. Any continuous change of position of one or both swimming legs, over a period of 4 consecutive frames was recorded as swimming leg waving behaviour. The point of onset and termination of each bout of swimming leg waving was also recorded.

Pattern 15

Locomotion type. This was recorded as the original locomotion type parameter.

Pattern 16

Direction of locomotion relative to opponent. As for Pattern 15, this was recorded as the original locomotion direction parameter (Parameter 9).

Pattern 17

Strike. As for Pattern 15, this was recorded as the raw variable (Parameter 14).

Pattern 18

Grasp. As for Pattern 17.

Pattern 19

Asynchrony of swimming legs in medial plane. This allowed a check to be made on the movements of the swimming legs and to detect if both legs moved in the same direction at the same time.

Pattern 20

Asynchrony of swimming legs in saggital plane. As for Pattern 19, this allowed a check to be made on differential positioning or movement of the swimming legs, forwards or backwards over the carapace (Figure 4.6).

Pattern 21

Asynchrony of chelipeds. Pattern 21 occurred at any point in which the two chelipeds of a crab were not in the same position.

In the discussion that follows, each of the behaviour patterns will be referred to as Pattern 'x'. Of necessity, text containing reference to a number of different patterns may become complicated. For this reason, and in order to aid in the understanding of the text, a summary of patterns 1-21 is contained on a loose sheet inside the back cover of this thesis.

4-3 RESULTS

4-3.1 QUALITATIVE DESCRIPTION OF AGONISTIC BEHAVIOUR

Agonistic interactions are initiated by orientation of one crab towards the other. This usually results in the other crab raising itself from the substrate (if not already raised) and manoevering so that both interactants face each other. At this stage both the chelipeds and the fifth pereiopods (swimming legs) are raised and extended to one or other of the positions discussed previously (see 4-2.2) thereby increasing the frontal area presented to the opponent. On reaching this stage, a number of different paths may be followed and are outlined below.

1. Interactions decided by stationary display.

   Interactions of this type involve no ambulatory movement of either interactant prior to the final retreat of one individual. Changes in position of chelipeds, swimming legs, body angle and height may often occur during these displays. However, in some interactions, no movement of any description occurs between initial orientation and retreat of one individual.

2. Interactions decided by single approach - retreat.

   These interactions are characterised by a single approach by one crab resulting in immediate retreat by the other. This may be preceded by a period of stationary display and as with the mutual stationary display (1. above) change in position of chelipeds, swimming legs and body position may occur at any point in the interaction.

3. Interactions decided by alternating approach - retreat.

Interactions of this type involve periods of stationary display interspersed with two or more bouts of approach and retreat in which each crab retreats at some stage from its advancing opponent, before a contest is settled. Again, cheliped, swimming leg and body movement may occur at any point.

4. Interactions involving physical contact or escalated aggression.

Interactions of the type 1-3 above do not involve any physical contact between crabs, each interaction being settled at a signal level (Hazlett, 1966b). Escalated aggression however, involves an individual making physical contact with the other contestant. This takes the form of either striking or grasping the opponent as discussed previously (see 4-2.2). Movements of chelipeds, swimming legs and body position may occur before, during or after this escalated aggressive behaviour.

Table 4.3A shows the number of fights in each category and the mean and range of fight length. Figure 4.23A shows the cumulative distribution of fight lengths in each of the four categories. Of the 42 fights involving physical contact, 21 involved a single approach during which physical contact was made and 21 involved multiple approaches.

Figures 4.23 and 4.24 show flow diagrams of the main sequence of events during an interaction for winners and losers respectively. These figures represent a synthesis of information obtained from 107 paired interactions as described in 4-2.2. The type of display used by winners or losers is not considered at this stage but is discussed later.

Table 4.3a Distribution of fight length and SDI in each of the four fight categories (4-3.1).

Fight category	Number of fights	Fight length range (frames)	Mean fight length (frames)
1	14	14-156	51
2	41	8-144	39
3	10	22-266	76
4	42	8-212	48
	107		

Category	SDI Range	SDI mean
1	0.05-0.36	0.19
2	0.02-0.67	0.23
3	0.04-0.24	0.16
4	0.02-0.40	0.18

Category 1, Stationary display

2, Single approach/retreat

3, Alternating approach/retreat

4, Physical aggression

FIGURE 4.23a

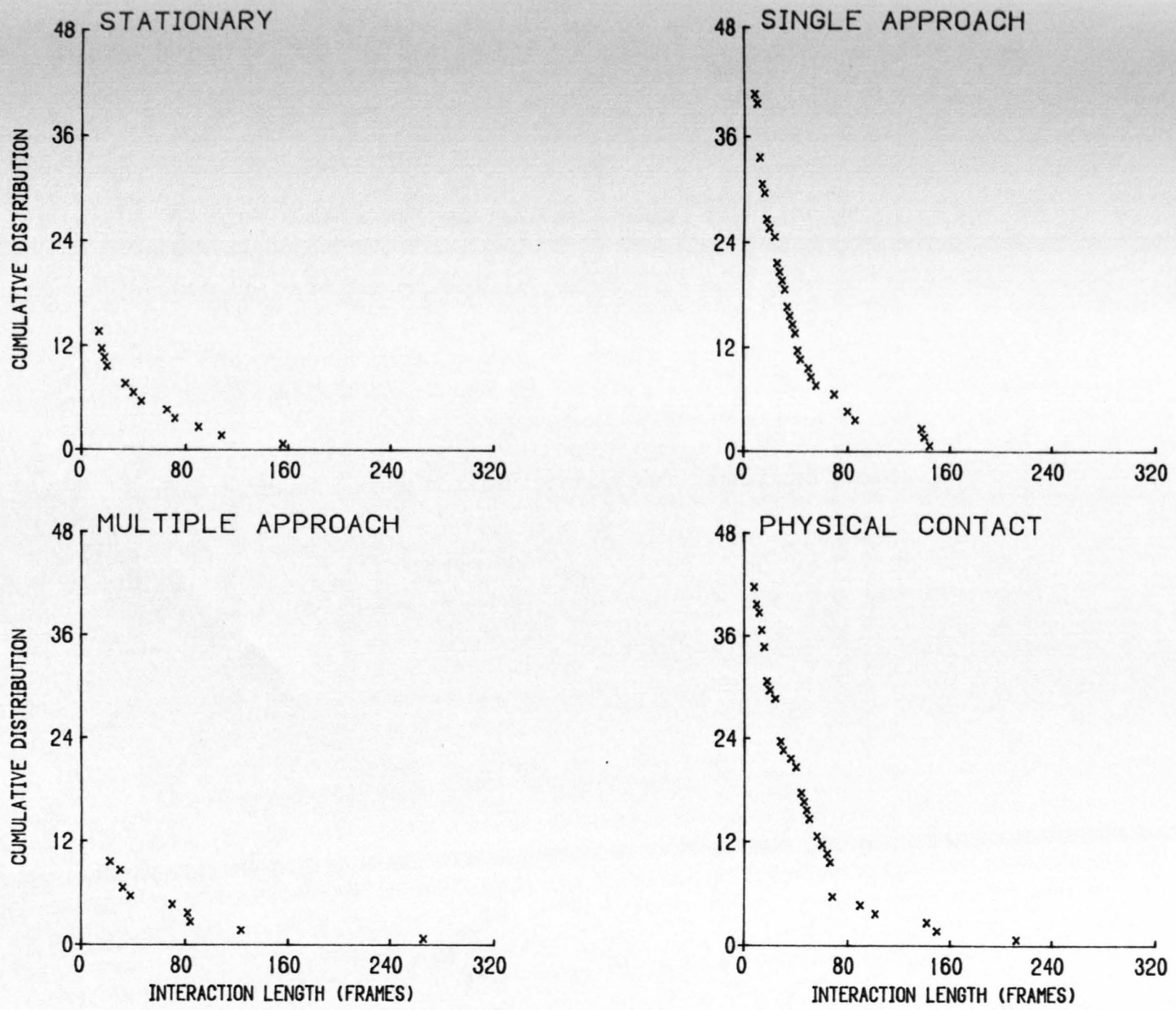
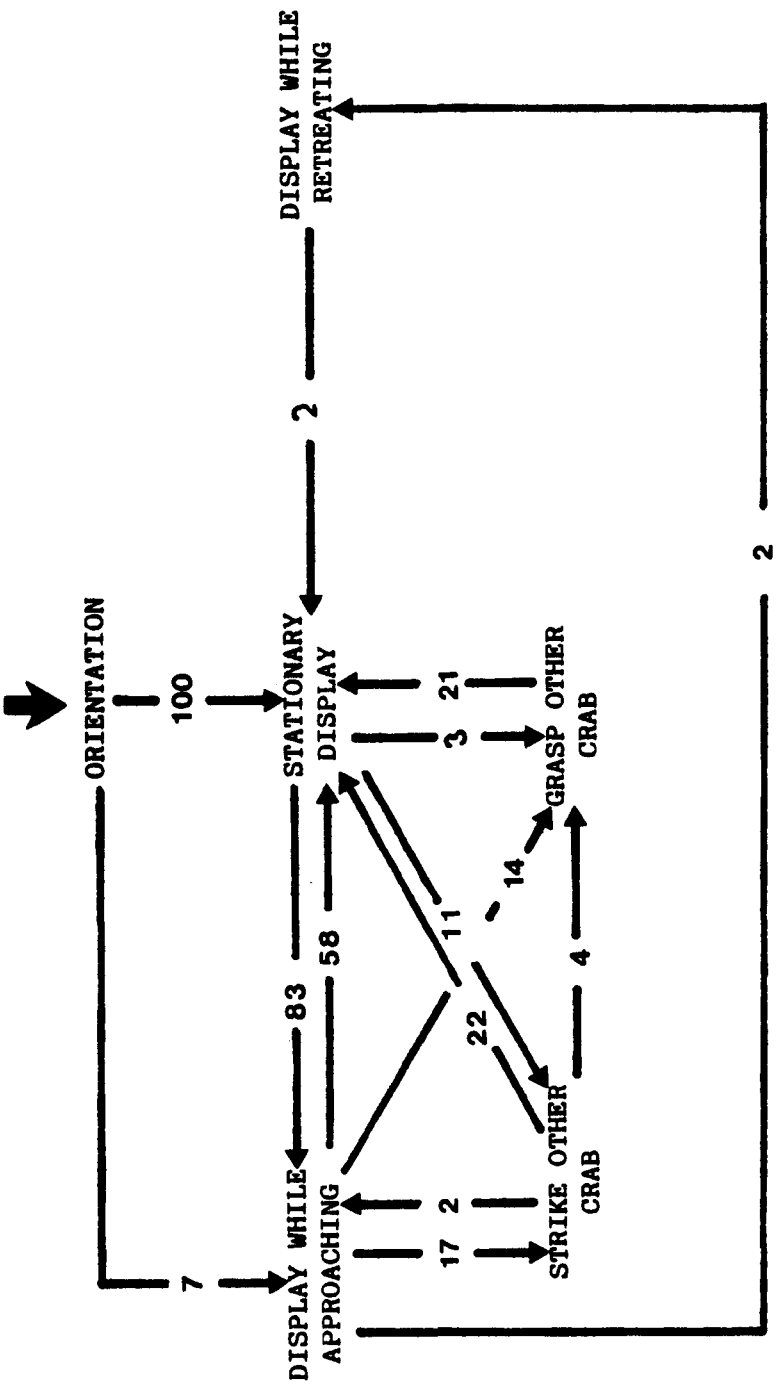


Figure 4.23a Cumulative distribution of fight length for each of the four categories of fight (4-3.1).

Figure 4.23 Flow diagram showing main sequence of events shown by winning crabs



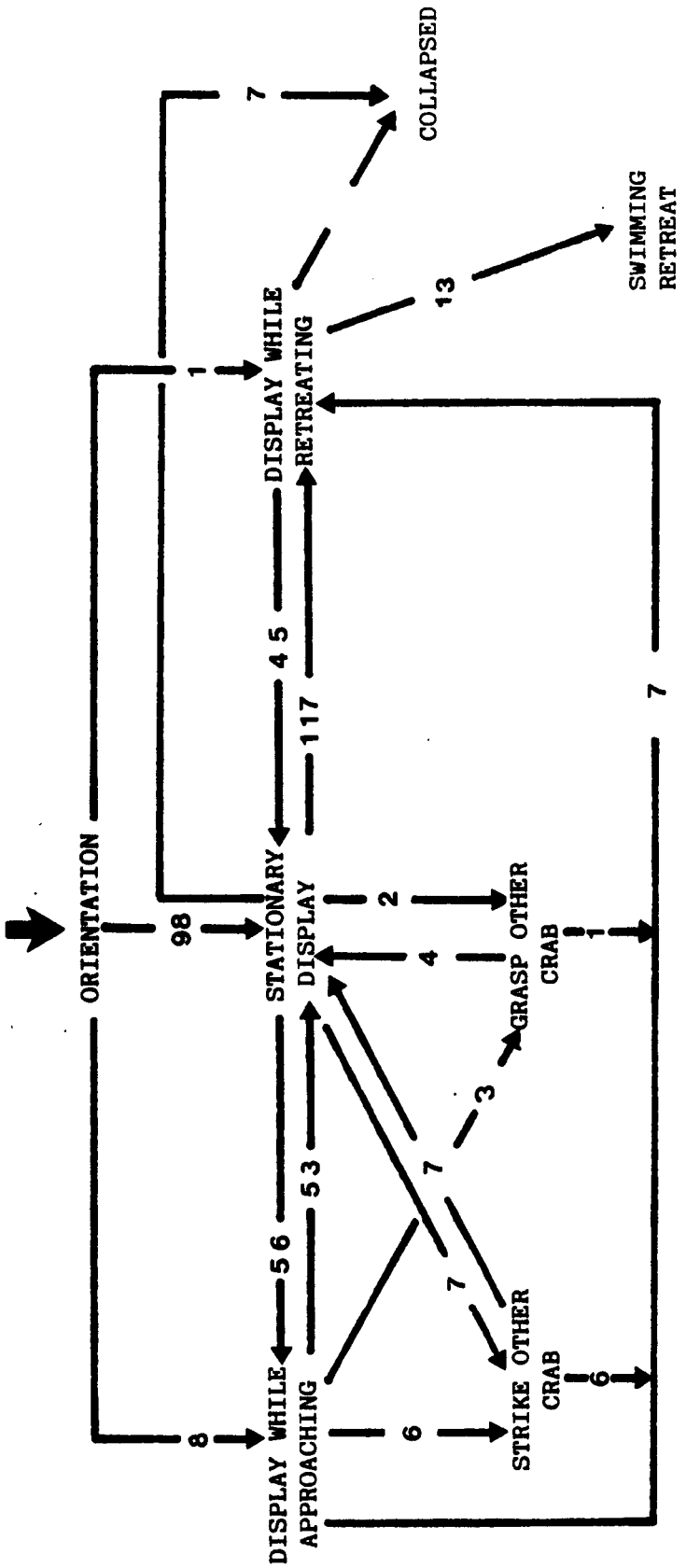


Figure 4.24 Flow diagram. Main sequence of events shown by losing crabs.

In the case of both winners and losers, the majority of animals moved directly into a stationary display on orientation to an opponent at the beginning of an interaction (Winners, 93%, N = 107; Losers, 92%, N = 107). In only one interaction did an individual retreat immediately from its opponent, without first passing through a stationary display stage. Subsequent to the initial stationary display stage, each interaction followed a series of approaching, retreating or stationary displays before culminating in the collapse of an individual or retreat from a stationary opponent, signifying the termination of the interaction. At this crude level of analysis, the sequence of behaviour appears remarkably similar for both winning and losing crabs. However, examination of Figures 4.23 and 4.24 reveals a number of statistically significant differences. Winning crabs were more likely to move from a stationary display to an approaching display than were losing crabs ($x^2 = 5.24$, $p < 0.05$). In addition, no winning crab was observed to revert from a stationary display to a retreating display. This was observed frequently in losing crabs. Overall, winning crabs were also more likely to strike their opponents ($x^2 = 5.48$, $p<0.05$) and also after an approaching display ($x^2 = 5.26$, $p < 0.05$). There was no significant difference between winning and losing crabs in terms of grasping an opponent while engaged in a stationary display ($x^2 = 0.88$, N.S.). However, winning crabs grasped their opponents more often than losing crabs ($x^2 = 9.8$, $p < 0.01$).

Figures 4.25 and 4.26 present the above information re-arranged into behaviour sequences shown by crabs responsible for the initiation of an interaction and by those crabs which responded to an initiator. As with winners and losers, a number of significant differences are obvious. Initiators were more likely to transfer from a stationary

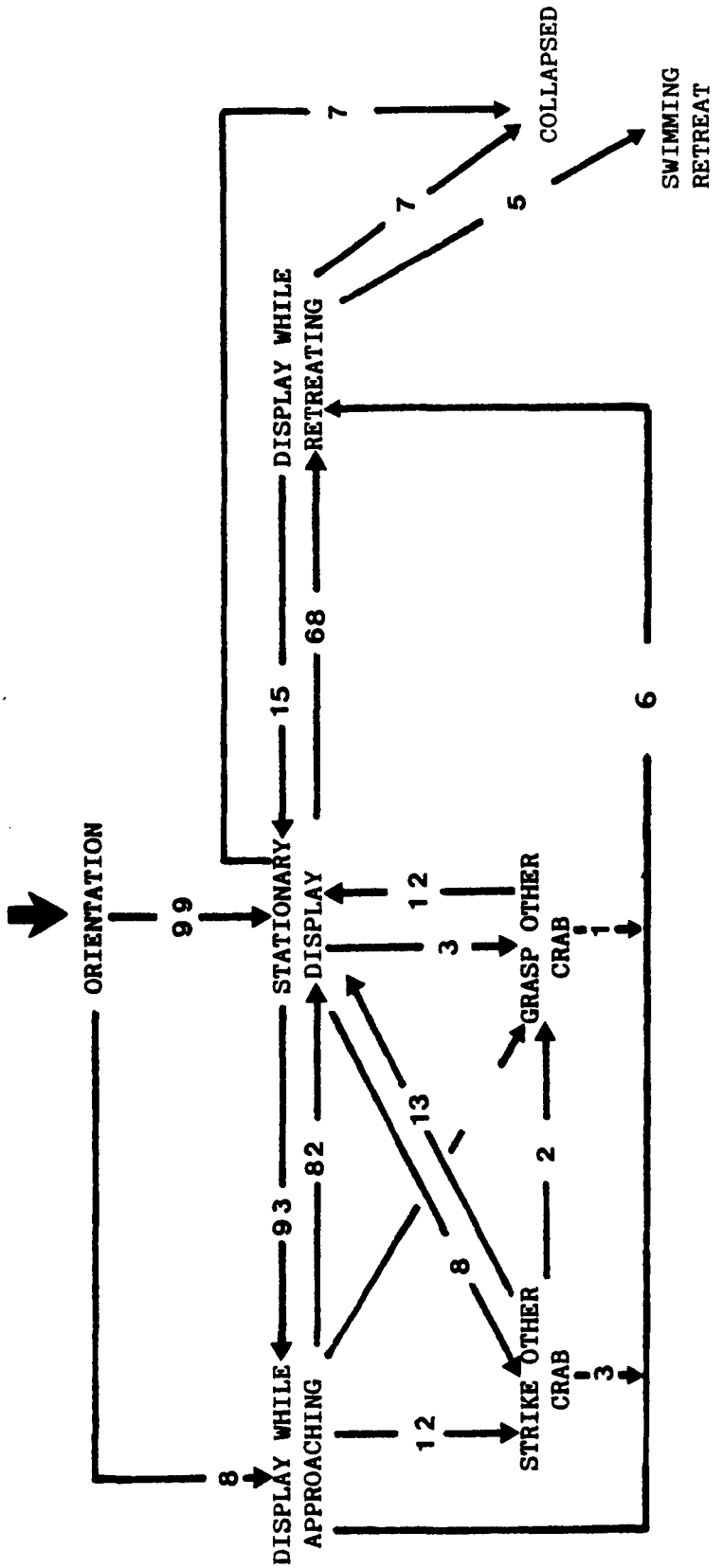


Figure 4.25 Flow diagram. Main sequence of events shown by crabs responsible for initiation of interactions.

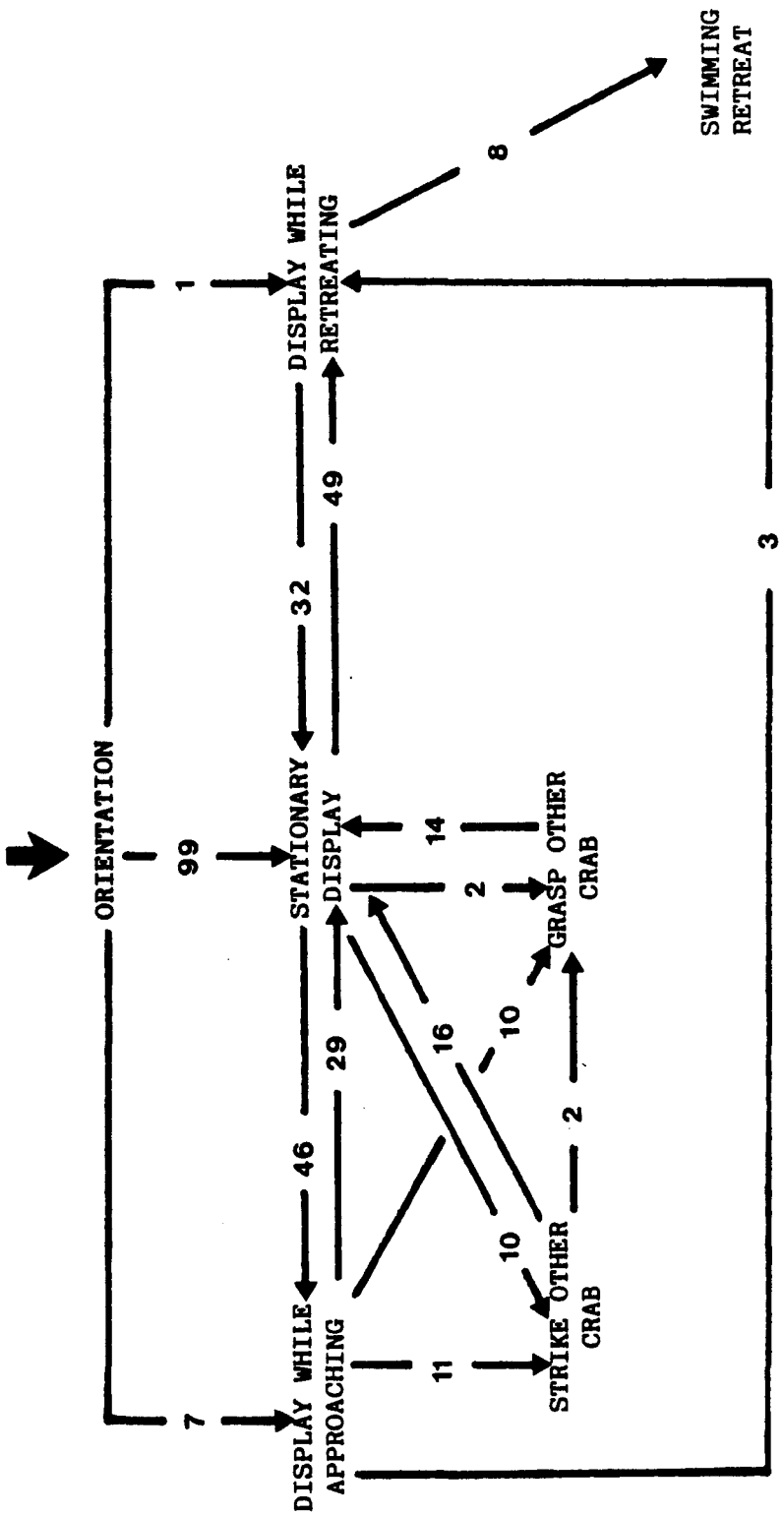


Figure 4.26 Flow diagram. Main sequence of events shown by responding crabs.

display to an approaching display, than responders (x^2 = 15.88, p $\prec$ 0.001). However, there was no significant difference between initiators and responders in the incidence of striking an opponent (x^2 = 0.024, N.S.) or of grasping an opponent (x^2 = 0.15, N.S.). In all other respects the sequence of behavioural events at this level is similar for both initiators and responders.

Table 4.3B shows the number of interactions in which each of the 11 main body postures (Pattern 1-11, see 4-2.3) were observed. There was no significant difference between winners and losers, or initiators and responders, in the number of interactions in which each pattern was observed (x^2 test, p $\prec$ 0.05). Similarly, no significant differences were observed with the initiator/responder data split into winning and losing categories.

4-3.2 BEHAVIOUR PATTERNS SHOWN BY ISOLATED INDIVIDUALS

Table 4.3a summarises the behaviour patterns shown by 5 isolated individual crabs, maintained under conditions identical to those employed for paired interactions. No crab showed any behaviour pattern with a frontal area larger than pattern 9 (i.e., Patterns 1-8). Figure 4.26a describes the sequence of behaviour shown by these crabs. Four of the five crabs remained stationary on the substrate while one (54 mm) alternated between slow walking and remaining stationary. All four crabs which remained stationary showed pattern 10 while the crab alternating between slow walking and remaining stationary, showed Pattern 9 and 10. In this case there did not

Table 4.3b Showing number of interactions in which each behaviour pattern was observed.

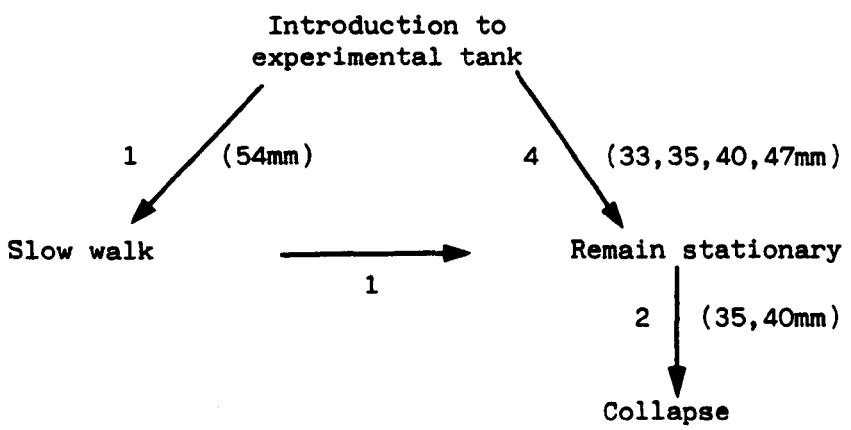
Pattern number	Winners	Losers		Initiators	Responders	
1	32	29	n.s.	38	23	n.s.
2	31	33	n.s.	31	33	n.s.
3	7	5	n.s.	9	3	n.s.
4	19	17	n.s.	20	16	n.s.
5	31	43	n.s.	38	36	n.s.
6	14	12	n.s.	14	12	n.s.
7	18	15	n.s.	16	17	n.s.
8	6	4	n.s.	3	7	n.s.
9	65	75	n.s.	70	70	n.s.
10	81	62	n.s.	75	68	n.s.
11	7	5	n.s.	6	6	n.s.
		X^2 test			X^2 test	

Table 4.3c Summary of behaviour patterns shown by five individual, isolated crabs.

Pattern number	Number of crabs showing pattern
1	0
2	0
3	0
4	0
5	0
6	0
7	0
8	0
9	2
10	4
11	0
	N= 5

One crab showed pattern 9 and pattern 10

Figure 4.26a Showing reactions of individual crabs when introduced to experimental tank.
The size of each crab is shown in parenthesis.



appear to be any relationship between walking and either pattern as both patterns were displayed while walking and while stationary. This individual continued to show behaviour patterns 9 and 10 throughout the recording period. Of the four crabs which remained stationary, two (35, 40 mm) collapsed to the substrate within 3 seconds of introduction to the tank and proceeded to bury themselves. The other two (33, 47 mm) held pattern 10 and spent the entire recording period sifting through the substrate with their chelipeds and occasionally transferring small particles to the mouthparts.

These results indicate that pairs of crabs react differently than do single crabs, when introduced into the experimental apparatus. As all other parameters were identical, this difference in behaviour must be caused by the presence of a conspecific and suggests that the behaviour shown in paried interactions represents response to the partner rather than response to some other aspect of the experimental situation.

4-3.3 DETERMINANTS OF INITIATION AND OUTCOME OF INTERACTIONS

Of the 107 interactions observed, 50 were initiated by the larger crab while 57 were initiated by the smaller crab in a pairing. Surprisingly, therefore, small crabs were just as likely to initiate an interaction as large crabs (x^2 = 0.92, 1 d.f., $p > 0.05$, N.S.). 47 interactions were won by the initiator while 60 were won by the non-initiator or responder. There is therefore no significant difference between

initiators and responders in terms of winning or losing an interaction (x^2 = 3.16, 1d.f., $p > 0.05$, N.S.). However, only 14 out of 107 interactions were won by the smaller of the two interactants, indicating that fights tend to be won by the larger of the interactants (x^2 = 116.65, 1 d.f., $p < 0.001$) (Table 4.4). In those interactions won by the smaller crab in a pairing, the SDI ranged from 0.02-0.34, ($\bar{x}$ = 0.16) suggesting that smaller crabs only won interactions when the difference in size between interactants was small.

4-3.4 INTERACTION LENGTH

Figure 4.27 shows the distribution of interaction lengths. Interactions ranged from eight frames in length (4 seconds) up to 266 frames (133 seconds) with a mean fight length of 48 frames (24 seconds) and standard deviation of 44. Figure 4.28 shows that if cumulative distribution of fight length is plotted, except for under-representation of very short fights, it follows the negative exponential curve as predicted by the War of Attrition model discussed by Caryl (1979). However, this does not take into consideration fight type or the fact that the size differential between interactants varied from interaction to interaction. Figure 4.29 shows fight length against size difference index (SDI). It is immediately obvious that there is a tendency for interactants with a small SDI (i.e., closely matched contestants) to interact for longer than pairs in which the SDI is large. However, this is further complicated, as the majority of fights (8 out of 11) greater than 100 frames in length, involved large size class individuals where the larger interactant was 50 mm or larger. It may therefore be the case

Table 4.4 Showing details of the initiation and outcome of interactions.

Size of crab	Initiator	Responder	
Larger	50	57	
Smaller	57	50	X^2=0.92, n.s.

Outcome	Initiator	Responder	
Winner	47	60	
Loser	60	47	X^2=3.16, n.s.

Outcome	Larger	Smaller	
Winner	93	14	
Loser	14	93	X^2=116.65, p<0.001

FIGURE 4.27 FIGHT LENGTH DISTRIBUTION

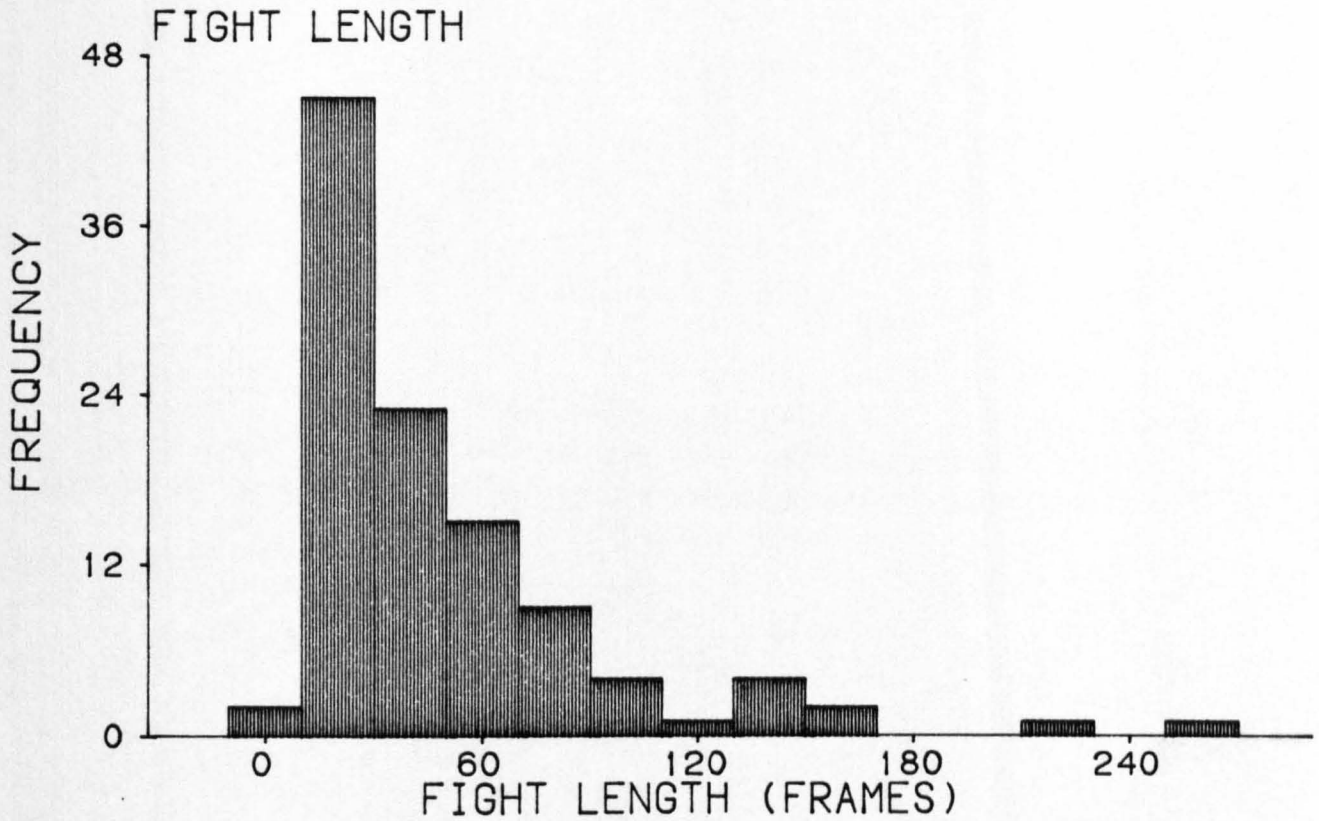


FIG. 4.28 CUMULATIVE DISTRIBUTION OF INTERACTION LENGTH

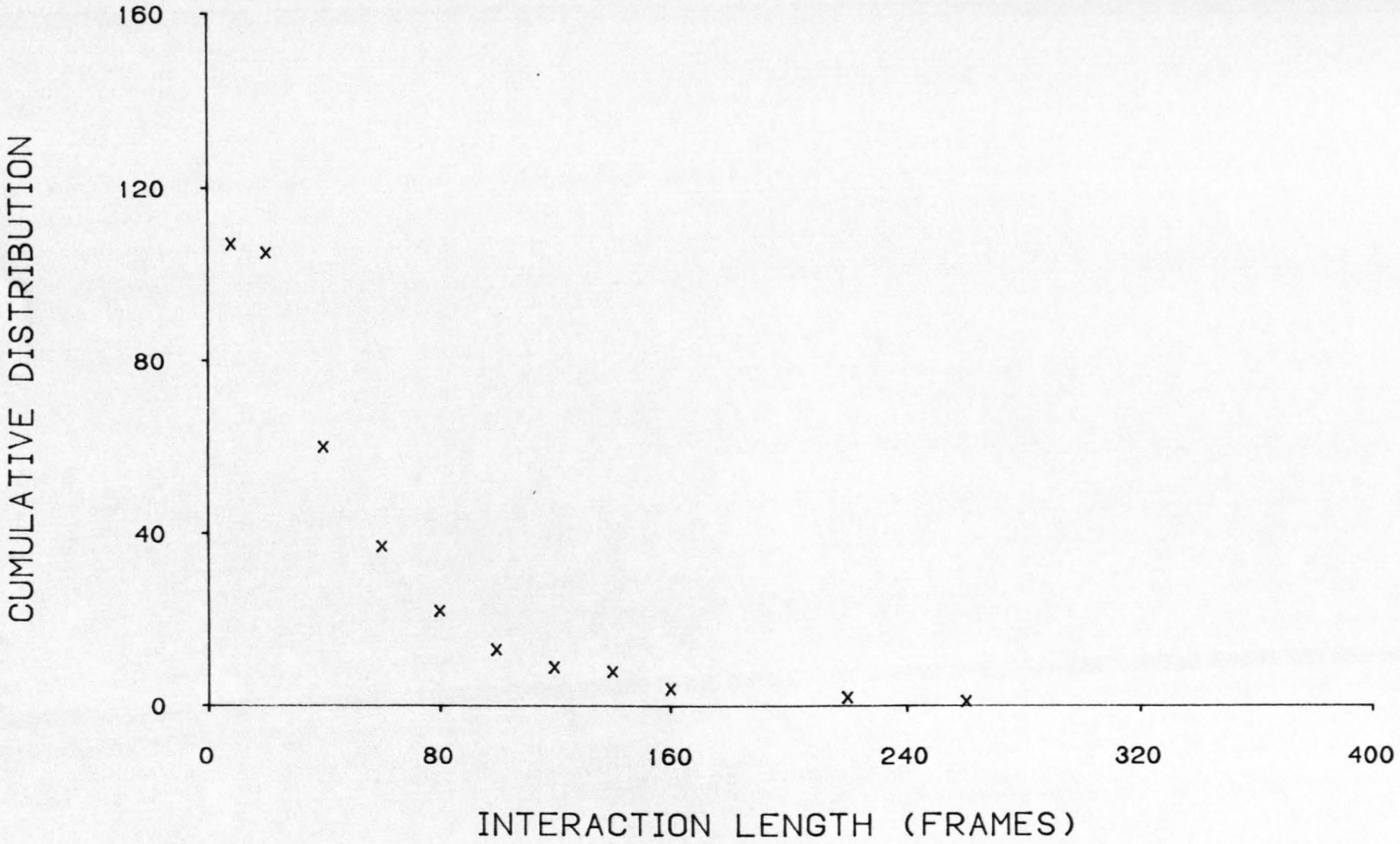
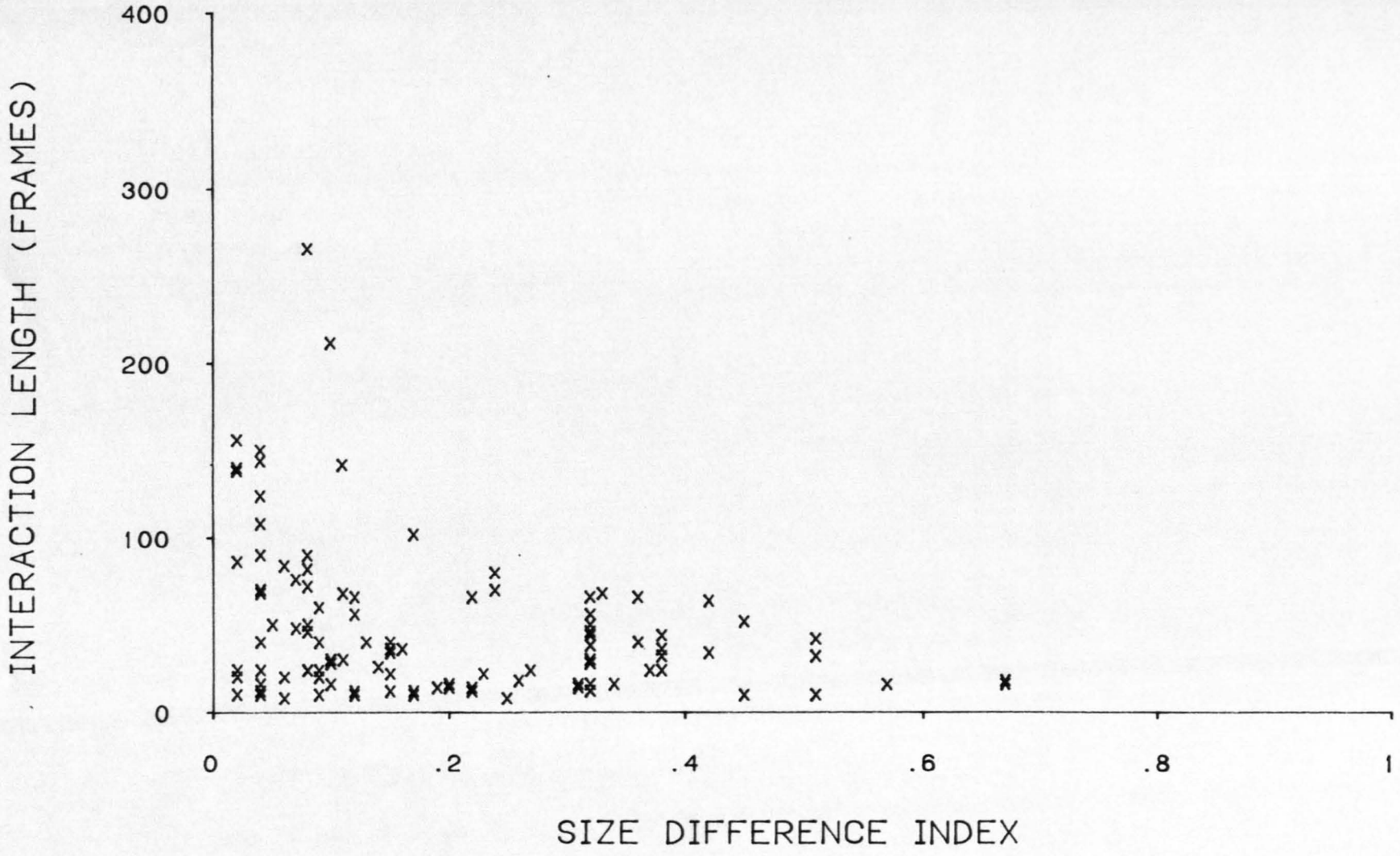


FIGURE 4.29 INTERACTION LENGTH VERSUS SDI



that larger crabs interact for longer than do smaller crabs. In order to investigate this possibility, each crab was arbitrarily defined as being large, medium or small. The following parameters were employed in order to obtain approximately equal numbers in each group; 48 mm, large; 42-47 mm, medium; 41 mm, small. Table 4.5 shows the mean interaction length for each of the six interaction categories. The interaction lengths were then compared (Mann-Whitney U test) with those of each other category of interaction (Table 4.6). Interactions involving 2 large size class crabs (L x L) were significantly longer than those involving one large and one medium size class crab (L x M), L x S, M x S and S x S, but not significantly longer than those involving two medium sized crabs (M x M, Table 4.6). This indicates that size differential as well as absolute size does have an effect on fight length. There were no significant differences in fight length between any of the other catetories. Interactions of the type L x L therefore last longer than those of any type except M x M. Regression analysis using fight length as the dependent variable and size of the larger crab, size of the smaller crab and SDI as the independent variables reveals that size of the smaller crab is the most important factor affecting fight length (see summary Table 4.7).

4-3.5 COMPARISON OF BEHAVIOUR SHOWN BY INDIVIDUAL CRABS FROM INTERACTION TO INTERACTION

Each of the multiple interactions shown in Table 4.2 was investigated to see whether individual crabs showed any consistent style of aggressive behaviour and if so, whether this differed from animal to

Table 4.5 Showing mean fight length and standard deviation for interactions involving large, medium and small size class crabs.

Interaction type	Number of interactions	Mean interaction length (frames)	Standard deviation
L*L	22	80	63
L*M	24	44	47
L*S	20	32	25
M*M	5	59	59
M*S	23	38	22
S*S	13	38	20

Table 4.6 Showing statistical differences in interaction length in fights between different categories of crab.

Interaction category	Interaction category					
	L*L	L*M	L*S	M*M	M*S	S*S
L*L	---	$p<0.05$	$p<0.01$	n.s.	$p<0.05$	$p<0.05$
L*M		---	n.s.	n.s.	n.s.	n.s.
L*S			---	n.s.	n.s.	n.s.
M*M				---	n.s.	n.s.
M*S					---	n.s.
S*S						---

Mann-Whitney U-test

Table 4.7 Summary of regression analysis where fight length is used as dependent variable. SDI and fight length are correlated due to colinearity between size of the smaller crab and size difference index.

Independent variate (x) SIZE OF SMALLER
Dependent variate (y) INTERACTION LENGTH FRAMES

Data source file name F1.F

A.V.	d.f.	S of S	m.s.	v.r.	
Regression	1	21273.305122	21273.305122	11.974	***
Residual	105	186540.302355	1776.574308		
Total	106	207813.607477			

Independent variate (x) SIZE DIFFERENCE INDEX
Dependent variate (y) INTERACTION LENGTH FRAMES

Data source file name F1.F

A.V.	d.f.	S of S	m.s.	v.r.	
Regression	1	20210.483946	20210.483946	11.312	**
Residual	105	187603.123530	1786.696415		
Total	106	207813.607477			

Independent variate (x) SIZE OF LARGER
Dependent variate (y) INTERACTION LENGTH FRAMES

Data source file name F1.F

A.V.	d.f.	S of S	m.s.	v.r.	
Regression	1	1366.504398	1366.504398	0.695	N.S.
Residual	105	206447.103079	1966.162886		
Total	106	207813.607477			

animal. Figure 4.30 shows the distribution of body postures with frame number for the two crabs (41 mm and 31 mm) in Group A (Table 4.2) which were paired together on two different occasions. Patterns 1-14 and 17-21 are simple variables and at any point in an interaction each pattern is in one of two states, i.e., it is either shown or not shown. Patterns 15 and 16 (locomotion type and direction of locomotion relataive to opponent) on the other hand are more complex, continuous variables and at any point in time may exist in one of a number of states. In order to simplify the analysis, patterns 15 and 16 were omitted.

In both interactions (Figure 4.30), the larger crab was the winner but the behaviour patterns shown in the first interaction (top diagram) are quite different from those shown in the second (bottom diagram), for both crabs. However, while each individual behaves differently in its two interactions there is some suggestion that within a given interaction both interactants behave in a similar manner in the second interaction (Figure 4.30, bottom diagram). Figures 4.31-4.41 show similar representations of the behaviour patterns shown in all other multiple interactions from groups B-D (Table 4.2). No multiple interactions were recorded from groups E-H.

Figures 4.32 and 4.33 however show that some animals react in a similar manner in more than one interaction. Both interactions shown in Figure 4.32 follow an almost identical form even though a different crab won the encounter in each case. This similarity in behaviour pattern is also shown by one individual in Figure 4.33, and examination of Figures 4.34 to 4.41 shows that this trend exists throughout the majority of the multiple interactions observed.

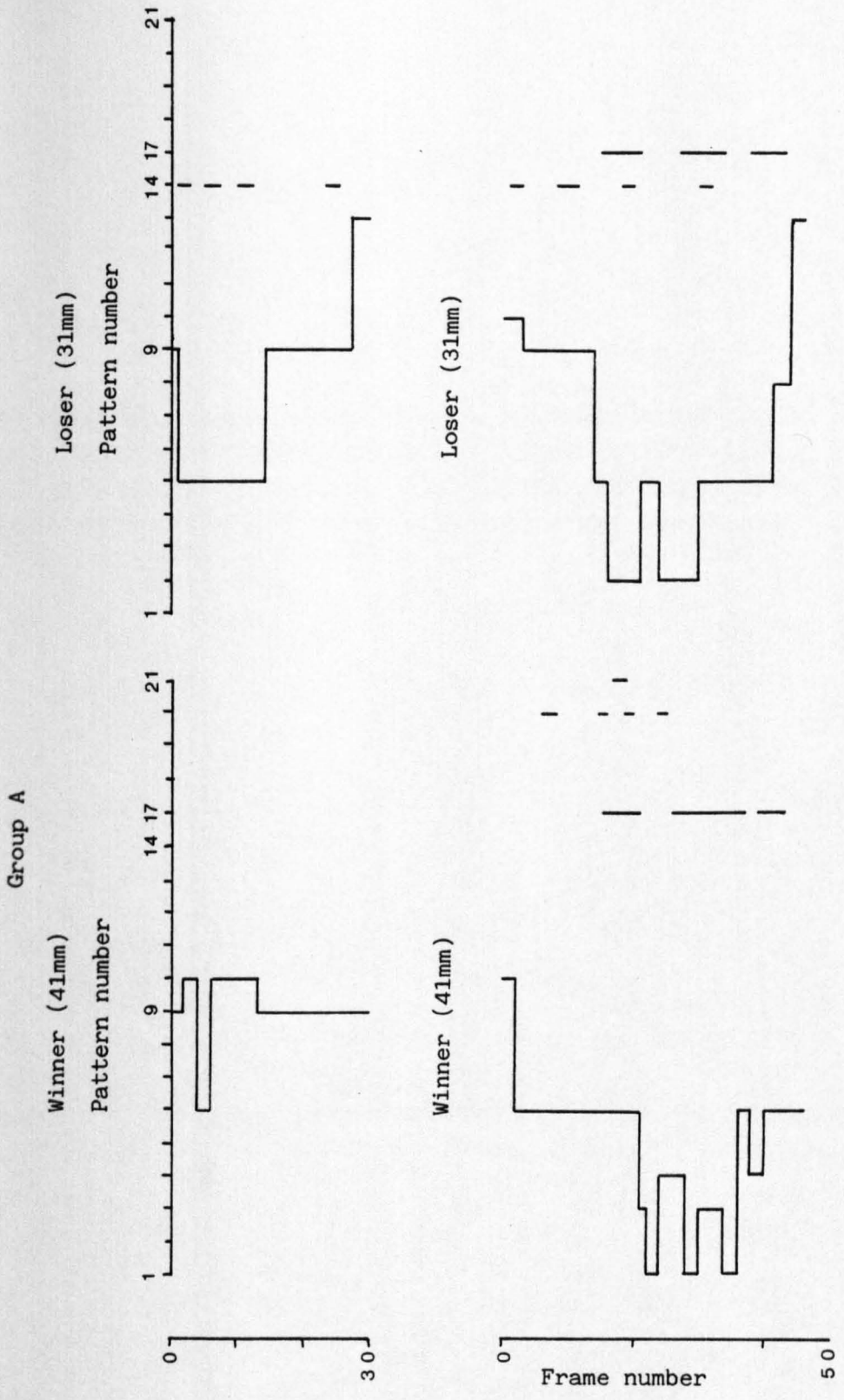


Figure 4.30 Fight profiles of multiple interactions in group A (see Table 4.2)

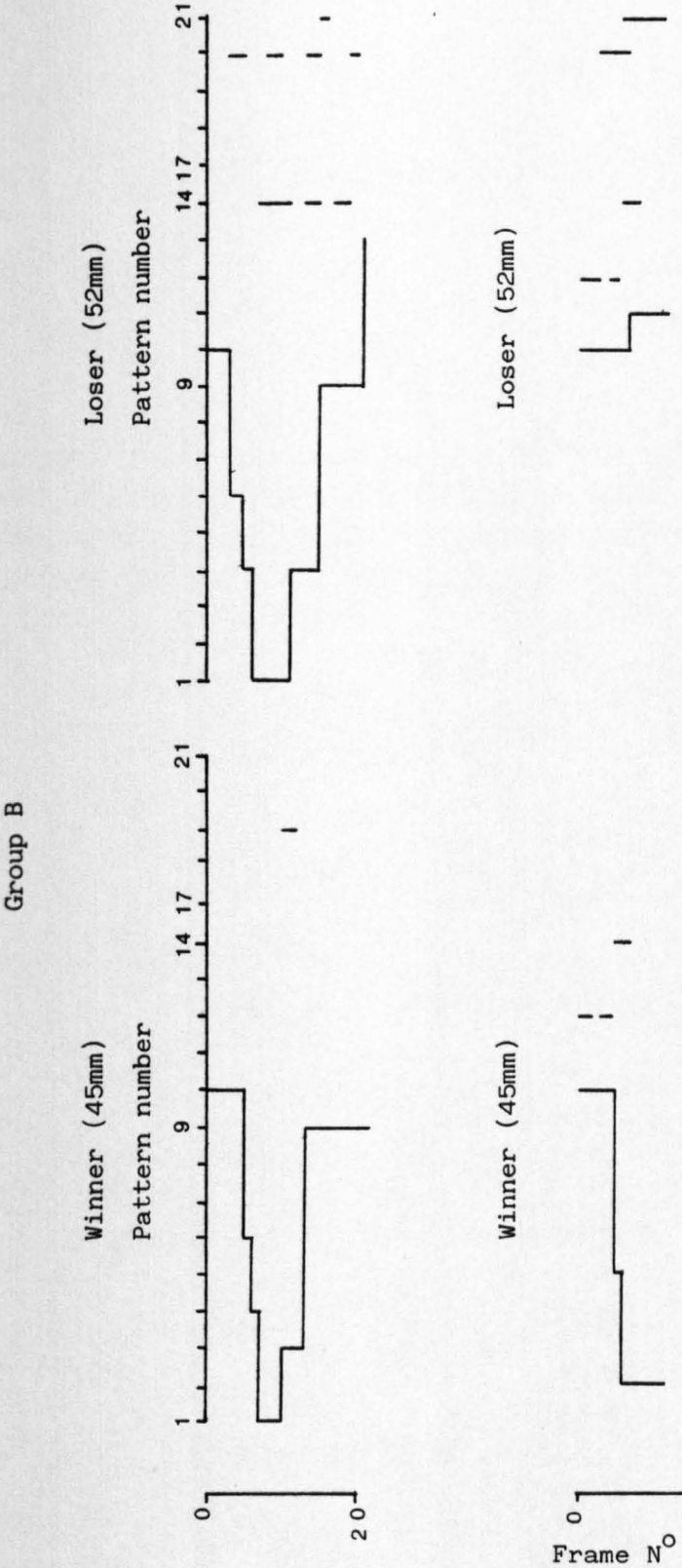


Figure 4.31 Fight profiles of Group B multiple interactions (see Table 4.2)

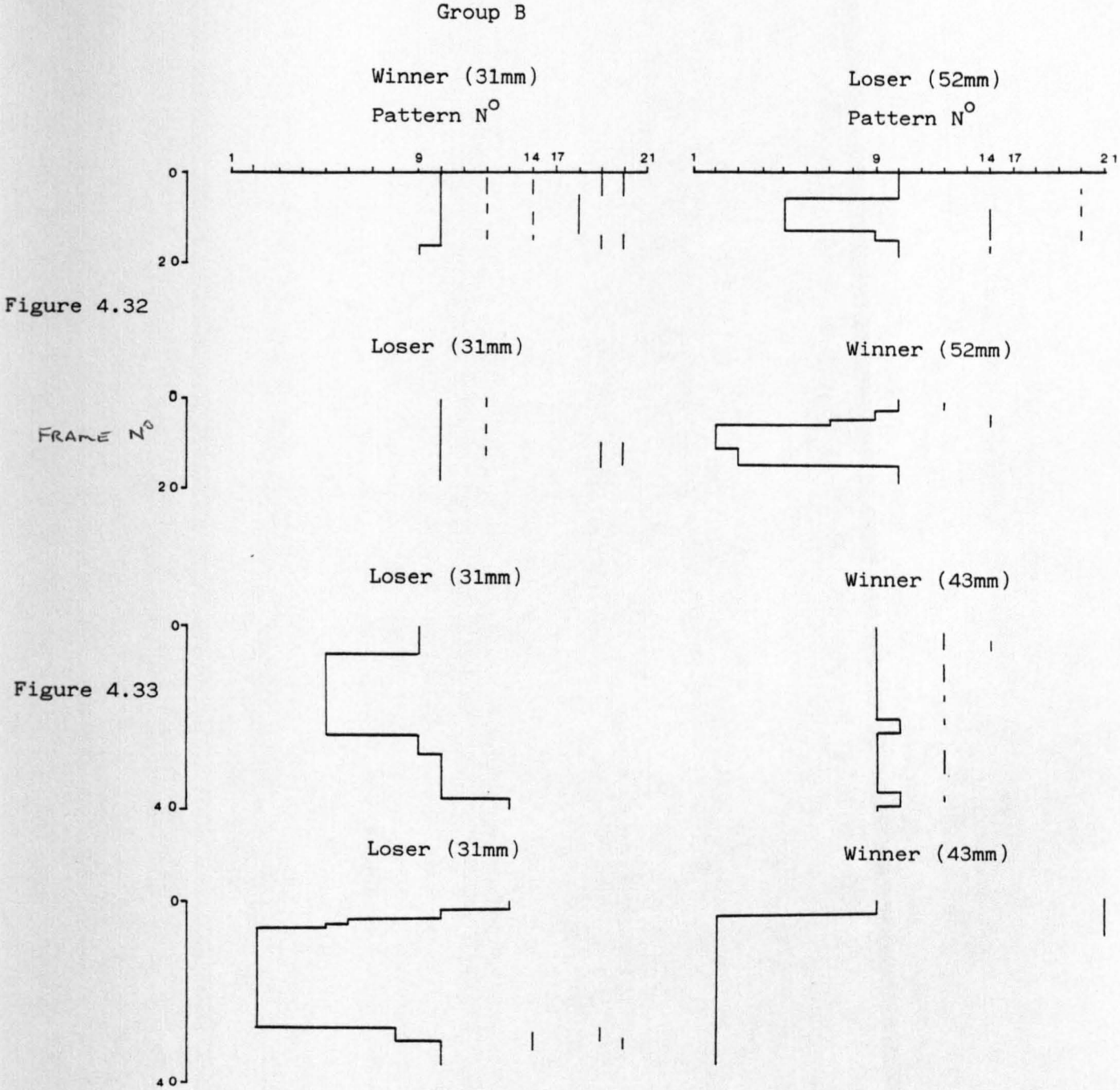


Figure 4.32

Figure 4.33

Figures 4.32 and 4.33 Fight profiles of Group B multiple interactions.

Group B

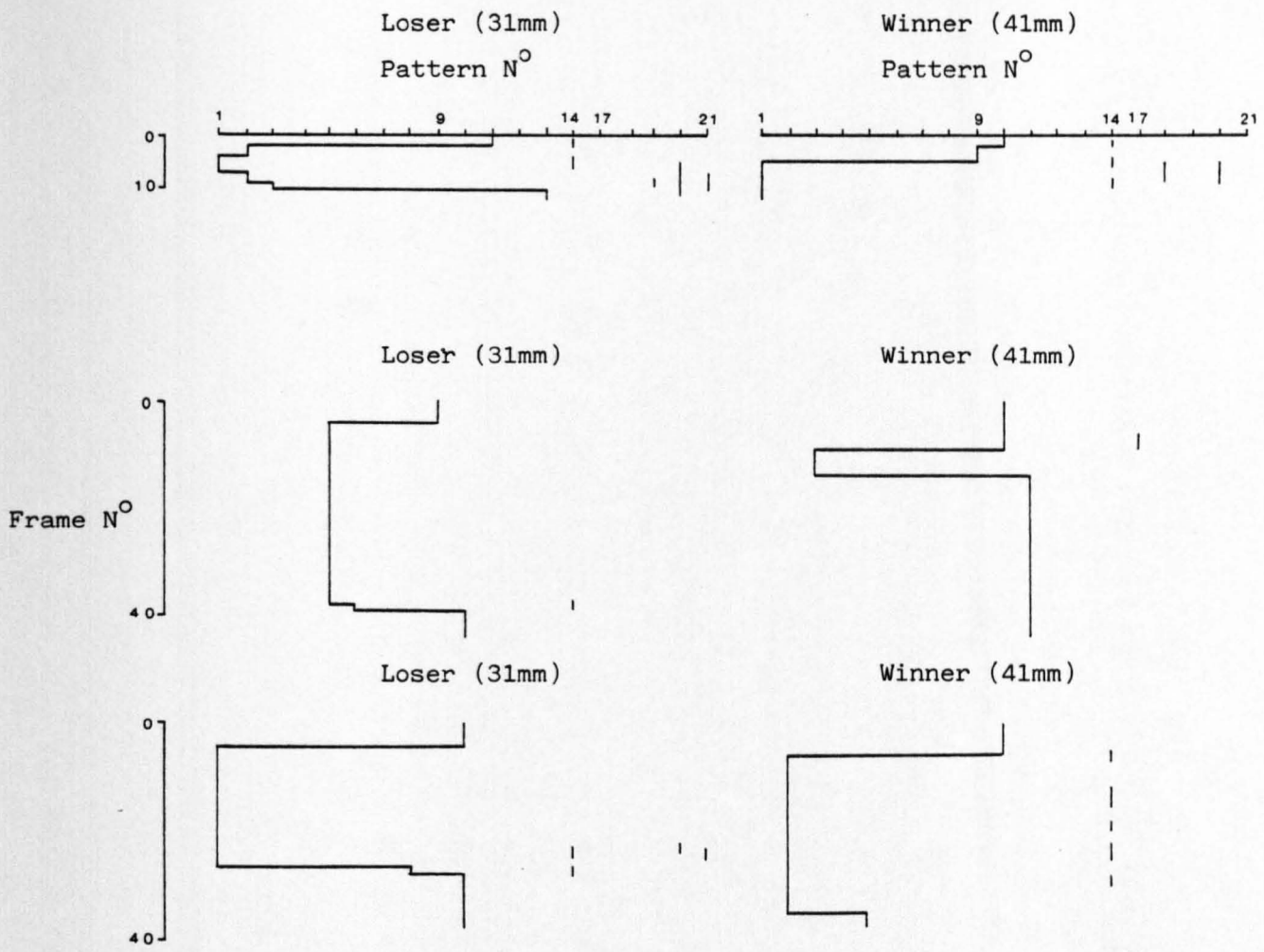


Figure 4.34 Fight profiles from Group B multiple interactions.

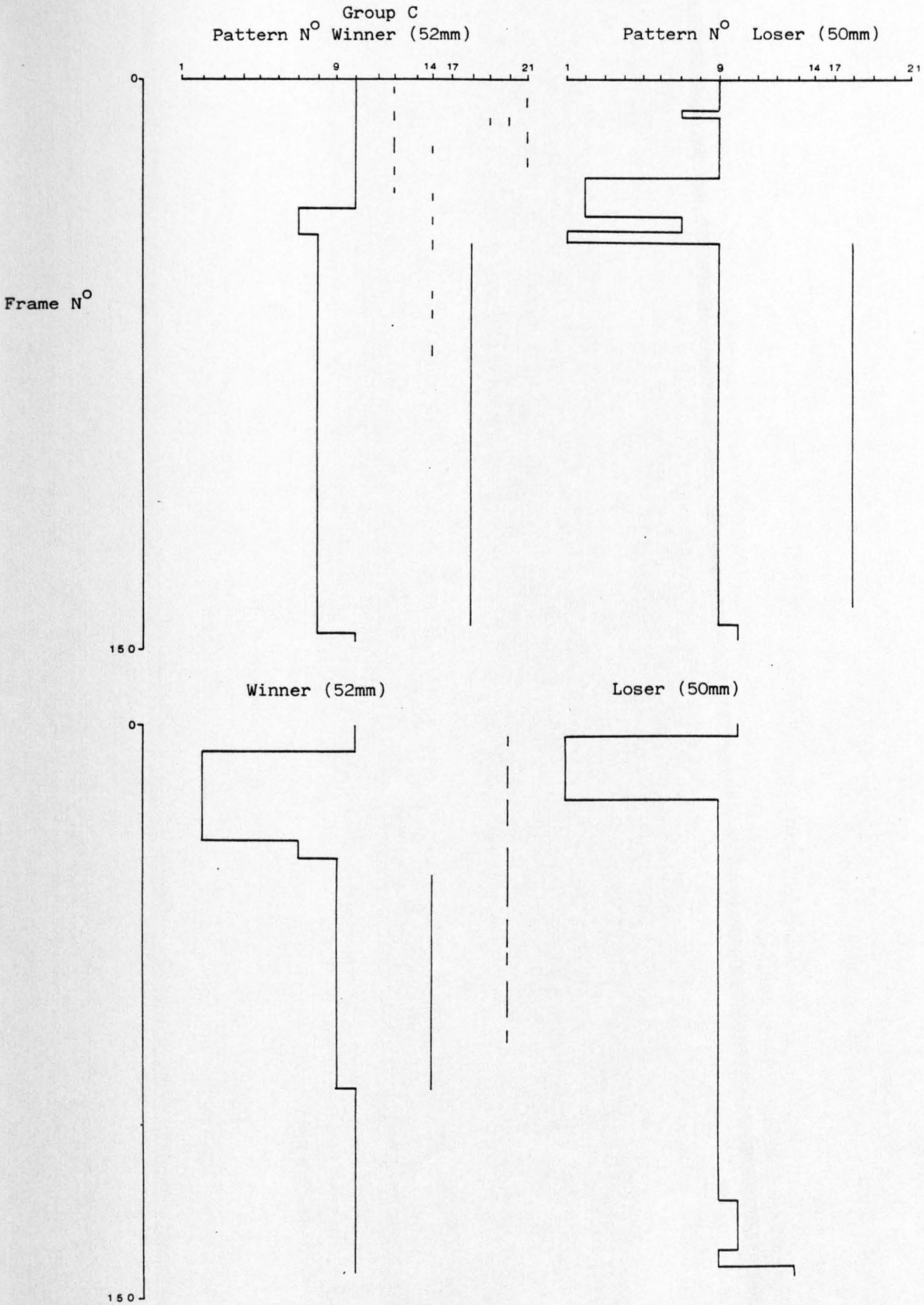
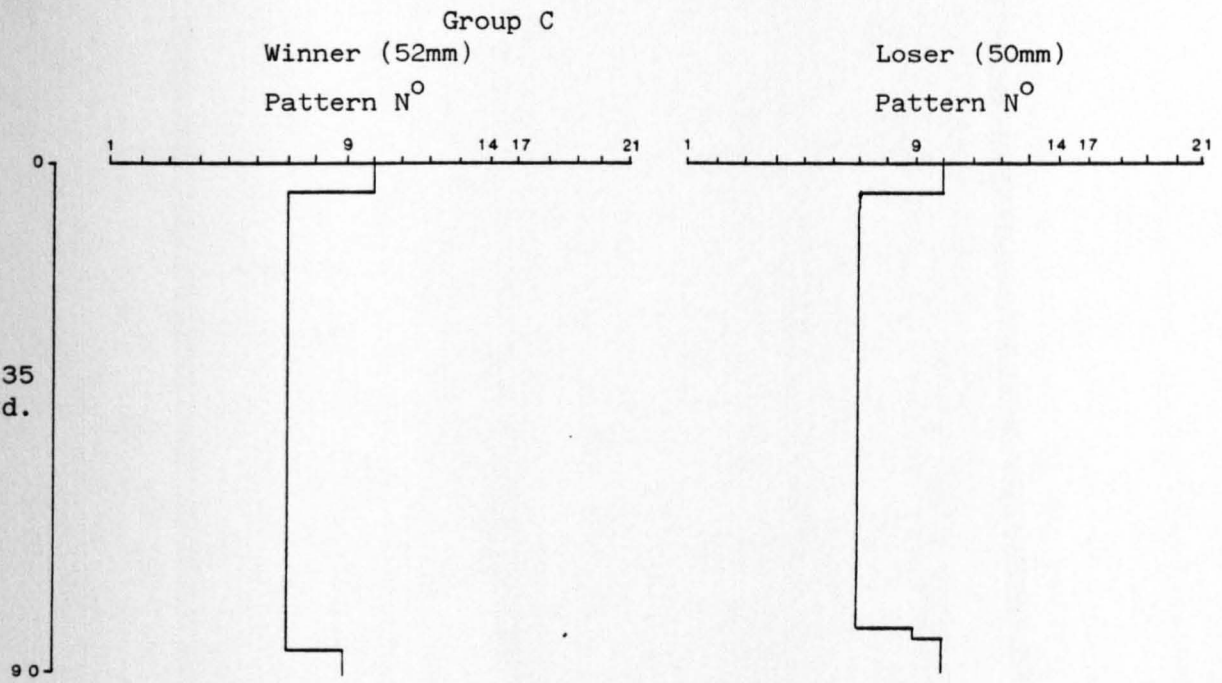


Figure 4.35 Fight profile from Group C multiple interactions.

Fig. 4.35 contd.



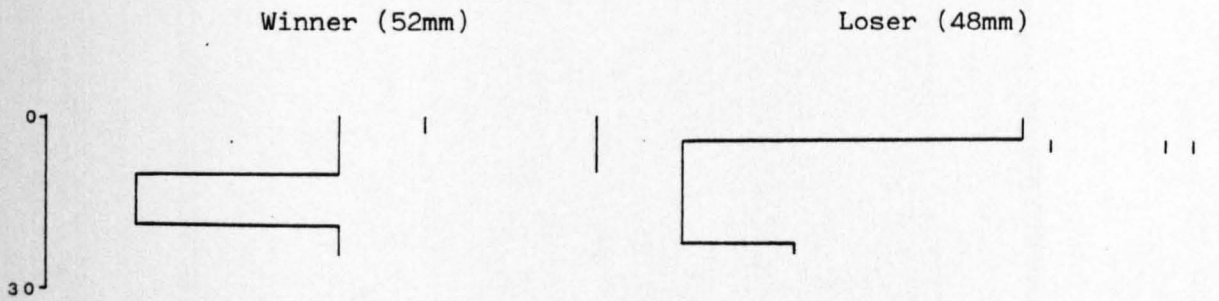


Fig. 4.36

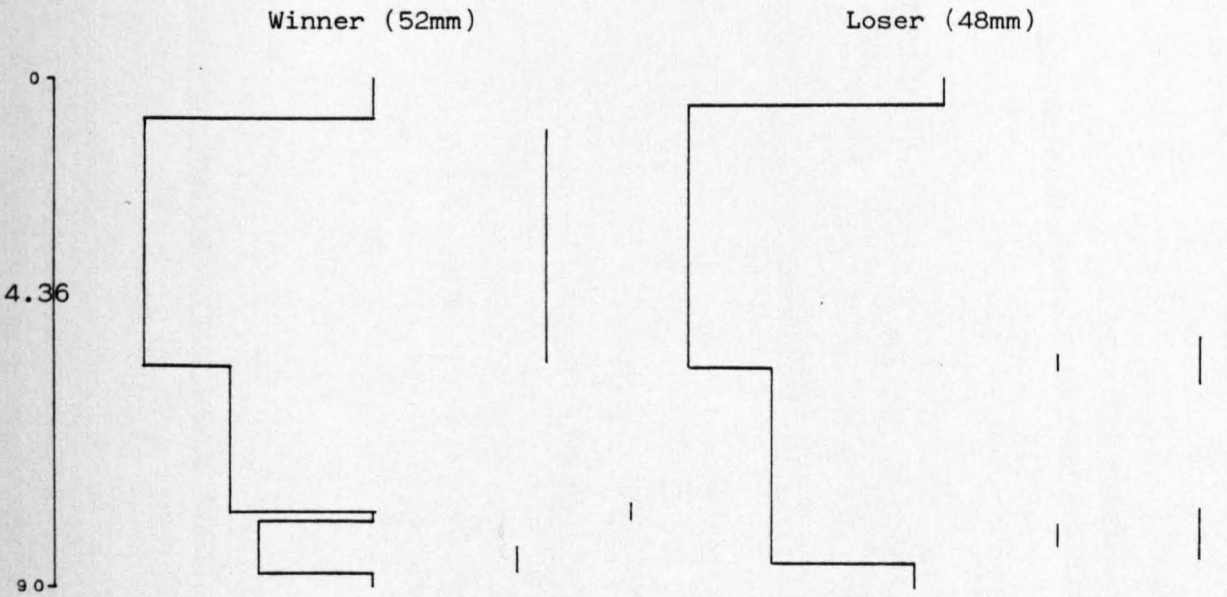


Figure 4.35 contd. and Figure 4.36 Fight profiles from Group C multiple interactions.

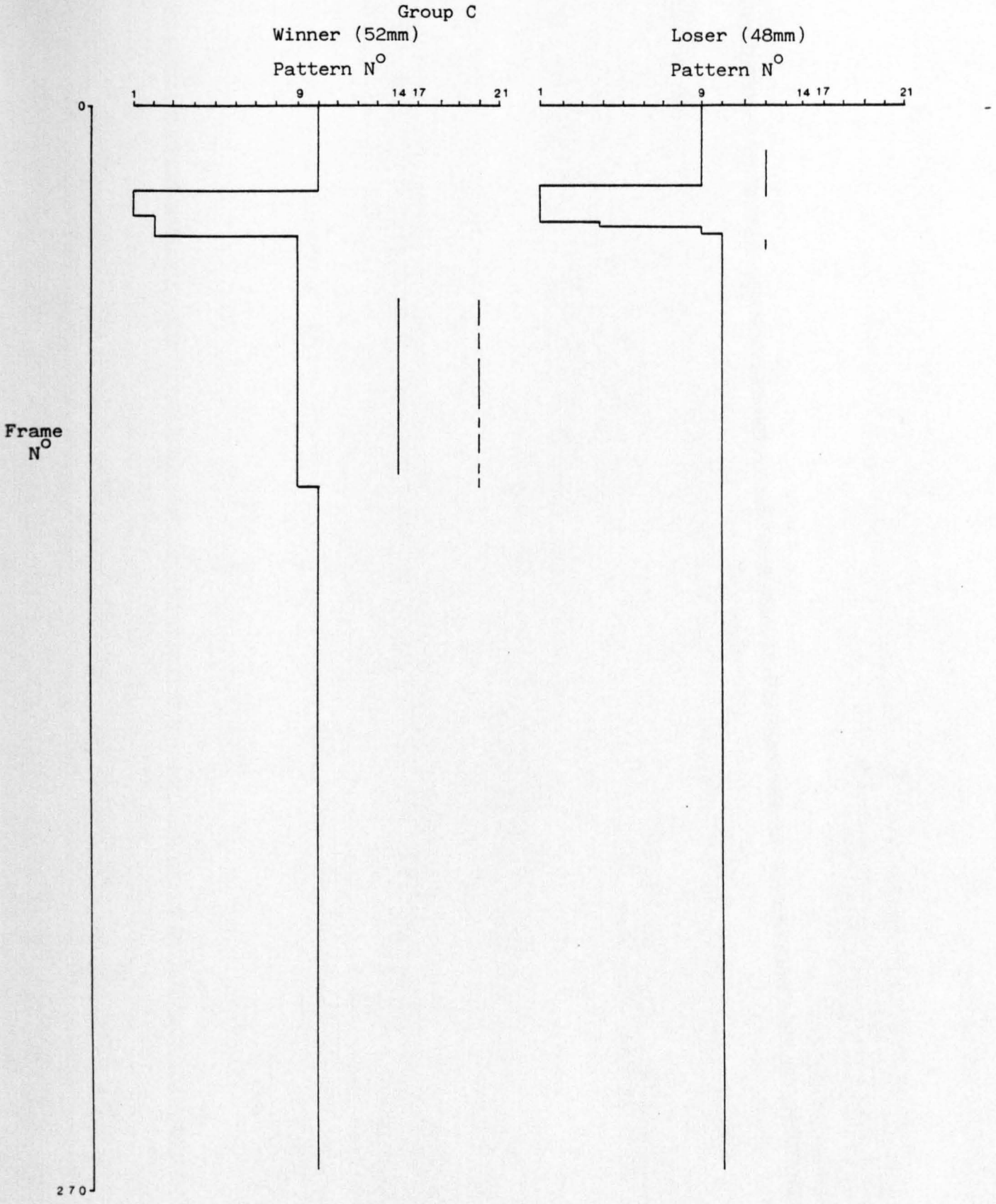


Figure 4.36 contd. Fight profile from Group C multiple interaction.

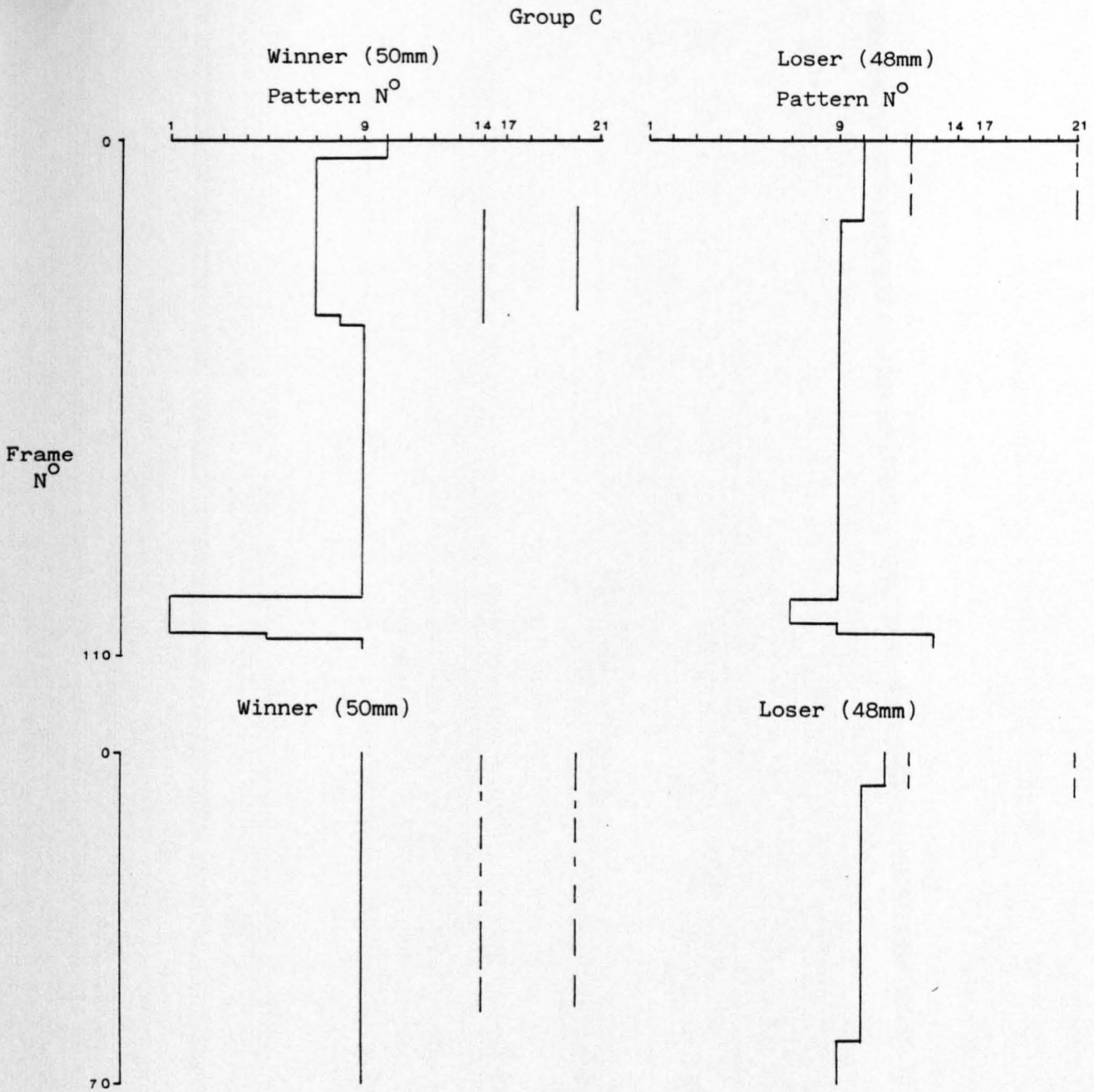


Figure 4.37 Fight profiles of Group C multiple interactions.

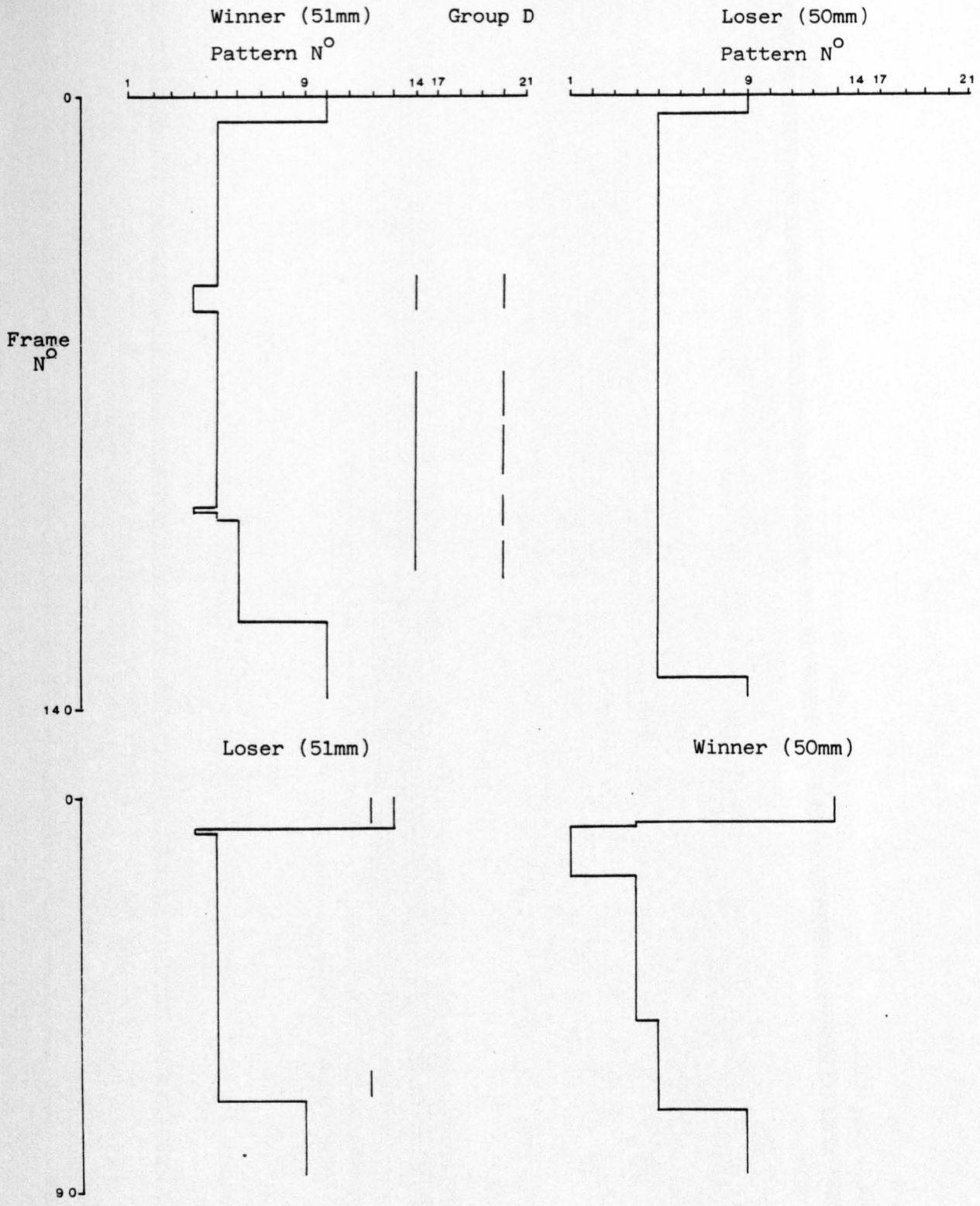


Figure 4.38 Fight profiles from Group D multiple interactions.

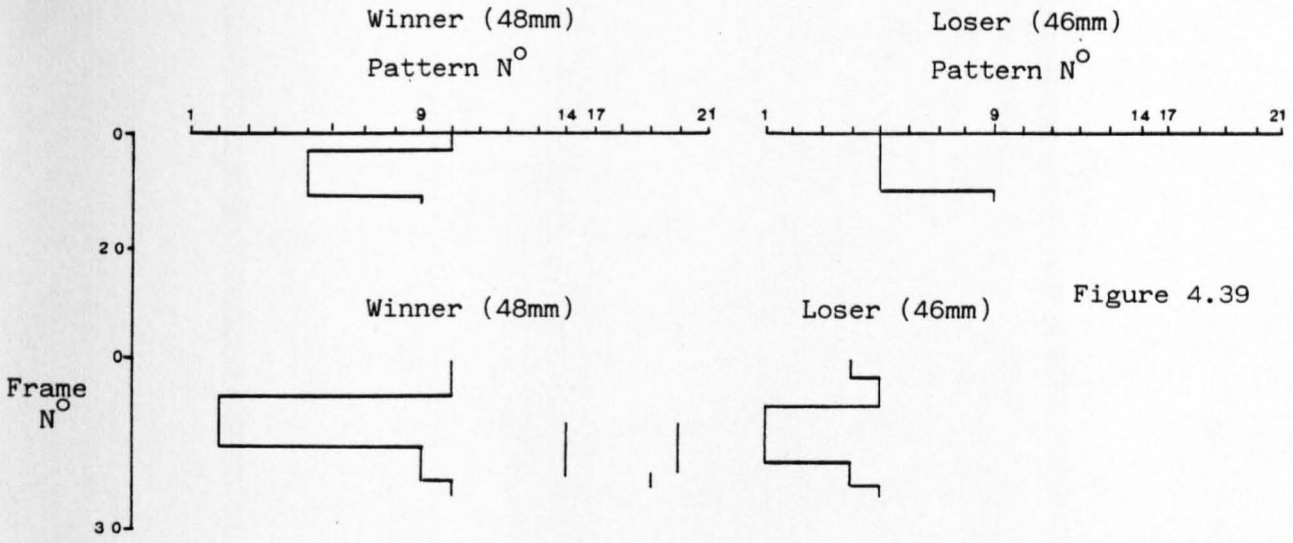


Figure 4.39

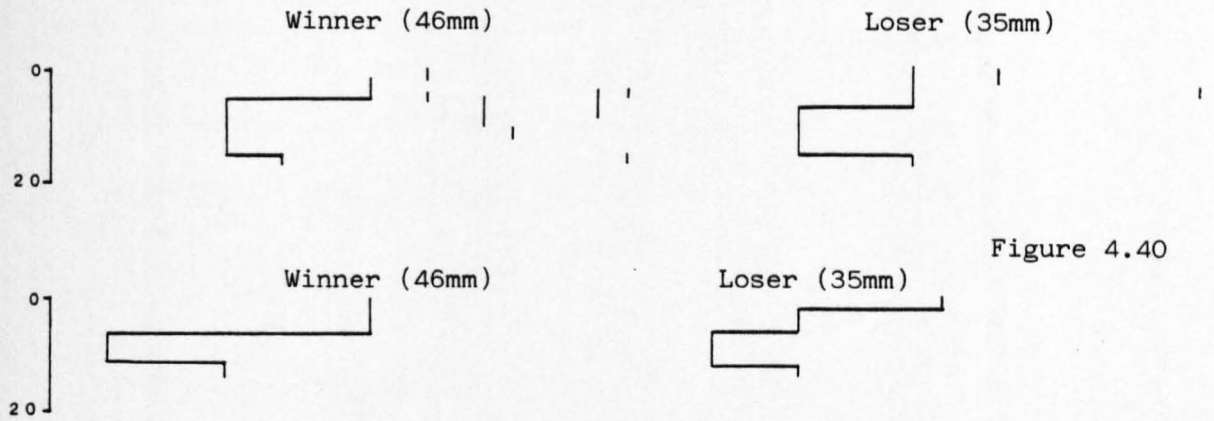


Figure 4.40

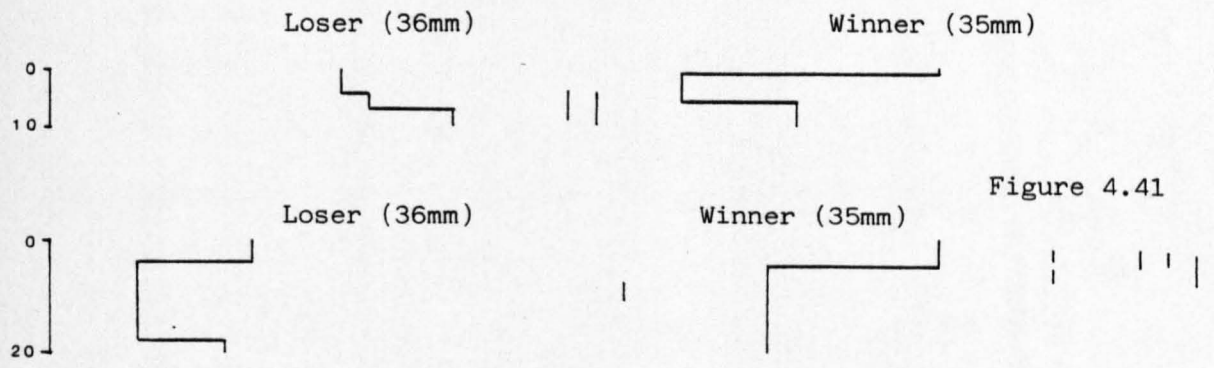


Figure 4.41

Group D

Figure 4.39 - 4.41 Fight profiles from Group D multiple interactions.

Further examination of the data gives no indication that crabs of a particular size tend to have similar fight profiles.

Two other interesting points arise from the diagrammatic representations. Both interactants within a given interaction show remarkably similar behaviour patterns irrespective of the SDI or the final outcome of the interaction. Examination of the raw data (personal observation) shows that this matching of behaviour is the case for most of the interactions recorded and not just the multiple interactions discussed in this section. The second point of interest is the similarity in interaction length when two crabs are paired together on more than one occasion. This trend is shown throughout Figures 4.30 -4.41.

These results suggest therefore, that individuals may react in a consistent manner from interaction to interaction. This in turn suggests that there is something about a particular combination of crabs which determines the form and duration of the fight. The results also indicate a remarkable similarity in behaviour between the 2 crabs in any given interaction, irrespective of which crab wins or loses.

4-3.6 ORGANISATION OF BEHAVIOUR WITHIN AN INTERACTION

In order that valid comparison may be made between fights of different lengths, each interaction was standardised as follows. For each crab, the cumulative total time spent showing each behaviour

pattern in an interaction was obtained. This value was then divided by the total interaction time thereby standardising for interaction length. These values (rates) were stored on computer file and employed in all subsequent analysis.

Interactions of different catgeories were then grouped together and these groups compared using Mann-Whitney U-test in an attempt to identify if the different categories were reflected in the proportions of behaviour patterns shown. Comparing long fights with intermediate length and short fights (as defined previously) some significant differences were observed in the proportions of the behaviour patterns. These results are summarised in Table 4.8. Although Table 4.8a shows that differences were observed between all categories these differences were minor and in no way represent major differences in organisation within an interaction. This is also true for the results depicted in Tables 4.8b-4.8d.

Taking the overall results for interactions of different lengths (Table 4.8a), the only difference between long fights and intermediate length fights was in the rate of swimming leg movement (Pattern 14), the rate being higher ($W = 3805.0$, $p < 0.05$) in intermediate length fights. No other differences were observed between these categories. Comparing intermediate length fights with short fights, again only one difference was observed. Intermediate fights showed a higher rate of Pattern 9 ($W = 7333.5$, $p < 0.05$) than did short fights. However, differences occurred in the rate of three patterns between long fights and short fights. Long fights showed a higher rate of occurrence of Pattern 2 ($W = 4338.5$, $p < 0.05$) and Pattern 9 ($W = 4485.0$, $p < 0.01$) while short fights showed higher rates of swimming

Table 4.8 Summary table;comparison of rates of behaviour patterns between different categories of crab.

* indicates significant differences while numbers in parenthesis indicate those pattern numbers which are significantly different.

Table 4.8a

	Fight length		
	Long	Intermediate	Short
Long	--	* (14)	* (2,9,14)
Intermed.		--	* (9)

Table 4.8b

	Winning Initiators	Winning Responders	Losing Initiators	Losing Responders
W.I.	--	n.s.	* (10,13)	* (10,13)
W.R.		--	* (12,13)	* (13,18)
L.I.			--	n.s.
L.R.				--

Table 4.8c

	Long Init.	Long Resp.	Inter. Init.	Inter. Resp.	Short Init.	Short Resp.
L.I.	--	n.s.	n.s.	n.s.	* (9)	n.s.
L.R.		--	n.s.	n.s.	n.s.	* (2,14)
I.I.			--	n.s.	* (9)	n.s.
I.R.				--	n.s.	n.s.
S.I.					--	n.s.
S.R.						--

Table 4.8d

	Long Winners	Long Losers	Intermed. Winners	Intermed. Losers	Short Winners	Short Losers
L.W.	—	* (10,14) (19,20)	* (5)	n.s.	n.s.	n.s.
L.L.		—	n.s.	* (12,13) (14,19)	n.s.	* (9,12) (13,14)
I.W.			—	* (5,12,13)	* (9,10)	n.s.
I.L.				—	n.s.	n.s.
S.W.					—	* (10,13)
S.L.						—

leg movement (Pattern 14, W = 3326.5, $p < 0.01$). In all other respects, long, intermediate and short length interactions showed similar organisation.

The results obtained when the data were split into winning, losing, initiating and responding categories (Table 4.8b), were similar to those discussed above, in that very few differences were observed in the organisation of interactions, but any differences which did occur were of a different nature to those shown in Table 4.8a. Winning initiators and losing initiators differed with respect to the occurrence of Patterns 10 and 13. Winning initiators showed a higher rate of Pattern 10 (W = 2911.0, $p < 0.05$) while losing initiators showed a higher rate of Pattern 13 (collapsed, W = 2137.0, $p < 0.05$). Similar results were obtained when winning initiator and losing responder categories were examined (Pattern 10, W = 2513, $p < 0.05$; Pattern 13, W = 1699.5, $p < 0.001$).

Winning responders and losing initiators differed with respect to Patterns 12 and 13, with winning responders showing a higher rate of feeding movements (Pattern 12, W = 4124.5, $p < 0.01$) and lower occurrence of Pattern 13 (collapsed, W = 3220.5, $p<0.05$), while winning responders showed a lower occurrence of collapse (Pattern 13, W = 2617.0, $p< 0.001$) and higher occurrence of grasping (Pattern 18, W = 3376.5, $p < 0.05$) than losing responders. These results shown in Table 4.8b again reflect very minor differences in the organisation of behaviour between interactants of different categories and in fact some of the differences (for example differences in Pattern 13 or collapse) reflect arbitrary distinctions as by definition winning crabs do not collapse after the initiation of an interaction.

Table 4.8c indicates that very few differences in organisation occur when long, intermediate and short length interactions are divided into initiating and responding categories and compared with each other. Minor differences were observed in only three of the 15 comparisons made. Long initiators showed a higher rate of Pattern 9 ($W = 1190.0$, $p < 0.01$) than short fight initiators; long fight responders showed a higher rate of occurrence of Pattern 2 ($W = 1164.0$, $p < 0.05$) and a lower rate of swimming leg movement (Pattern 14, $W = 782.5$, $p < 0.01$) than short fight responders; while intermediate length fight and short fight initiators differed with respect to the occurrence of Pattern 9, with intermediate fight initiators showing a higher rate of occurrence ($W = 1896.5$, $p < 0.05$).

Table 4.8d shows the results obtained when long, intermediate length and short interactions were split into winning and losing categories and each category compared with every other. Differences in organisation occurred in seven of the 15 comparisons made, but these may in part reflect the definition concerning winning and losing of interactions as discussed previously for the information in Table 4.8b. Long fight winners and losers differed with respect to the occurrence of Patterns 10, 14, 19 and 20 with the winners showing a higher rate of occurrence for all four patterns (Pattern 10, $W = 1072.0$, $p < 0.05$; Pattern 14, $W = 1100.0$, $p < 0.01$; Pattern 19, $W = 1063.0$, $p < 0.05$; Pattern 20, $W = 1061.0$, $p < 0.05$). Comparing winners of long interactions with winners of intermediate length interactions, no difference was observed in the rate of occurrence of any of the behaviour patterns except for Pattern 5, which was shown more frequently by winners of long interactions ($W = 1352.5$, $p < 0.01$). Losers of long fights and losers of intermediate fights however,

differed in a number of respects. Losers of long fights showed a higher rate of occurrence of feeding movements (Pattern 12, $W = 1286.5$, $p < 0.05$) while losers of intermediate length fights showed higher rates for collapse (Pattern 13, $W = 906.0$, $p < 0.05$), swimming leg movement (Pattern 14, $W = 843.0$, $p < 0.01$) and asynchrony of swimming legs in medial plane (Pattern 19, $W = 922.0$, $p < 0.05$). Similar differences were observed when long fight losers were compared with short fight losers. Long fight losers showed higher rates of Pattern 9 and feeding movements (Pattern 9, $W = 1140.5$, $p < 0.05$; Pattern 12 - feeding, $W = 1145.0$, $p < 0.05$) while short fight losers showed higher rates of body collapse (Pattern 13, $W = 784.5$, $p < 0.05$) and swimming leg movement (Pattern 14, $W = 754.5$, $p < 0.005$).

Comparing winners and losers in intermediate length interactions shows that winners show higher rates of Pattern 5 ($W = 1565.0$, $p < 0.01$) and feeding movements (Pattern 12, $W = 2130.0$, $p<0.05$) and by ddefinition, a lower rate of collapse (Pattern 13, $W = 1489.5$, $p < 0.001$).

Intermediate fight winners showed a higher rate of occurrence of Pattern 9 ($W = 1881.0$, $p < 0.05$) and a lower rate of Pattern 10 ($W = 1462.5$, $p < 0.05$) than short fight winners, while short fight winners showed a higher rate of Pattern 10 ($W = 1336.0$, $p < 0.05$) and a lower rate of body collapse ($W = 920.0$, $p < 0.01$) than short fight losers.

These results show that although some differences occur in the organisation of fights of different lengths and categories, these differences are minor and in part reflect the arbitrary definitions concerning the outcome of interactions.

4-3.7 CHANGE IN BEHAVIOUR DURING THE COURSE OF AN INTERACTION

In order to investigate how the behaviour of crabs changed during the course of an interaction, each interaction was divided into segments and the occurrence of each behaviour pattern in a segment was noted. Each interaction was arbitrarily divided into 10 equal length segments, and the plots of the number of interactions in which a behaviour pattern occurred versus segment of fight in which it occurred (for each behaviour pattern) are shown in Figure 4.42. Patterns 13, 15, 16, 19, 20 and 21 are not included in Figure 4.42. Pattern 13 (body collapse) was not included as by definition only losing crabs show this behaviour pattern signifying termination of an interaction. Patterns 15 and 16 (locomotion type and direction of locomotion relative to opponent) were not included as these also tend to be shown (by definition) at the beginning and termination of an interaction. Patterns 19, 20 and 21 were disregarded as they correlate very closely (see 4-3.8) with feeding movements and swimming leg movements (Patterns 12 and 14) which are discussed in this section.

Examination of Figure 4.42 shows that there are few clear cut, system-atic trends and that behaviour patterns tend to be shown evenly across all segments of an interaction. Patterns 9 and 12 (feeding movements) however, may be exceptions to this generalisation. Pattern 9 for winners, losers, initiators and responders is shown frequently during the first two segments of an interaction, decreases during the third and fourth segments before increasing in frequency again towards the end of an interaction. This suggests that

this position is a common starting and finishing posture for a crab to adopt and this is emphasised if Figures 4.30-4.41 are examined. Pattern 10 shows a similar effect but the trend is less marked than for Pattern 9. As for Pattern 9, Figures 4.30-4.31 show that Pattern 10 is a common posture during the opening and closing frames of an interaction.

Pattern 12 (Figure 4.42) is shown frequently during the first segment of a fight before falling off rapidly to a steady low level during the remainder of the interaction. This probably reflects one aspect of the experimental design. Pattern 12 is defined as feeding behaviour. Liquidised food was added to the experimental apparatus prior to introduction of the interacting crabs, in order to introduce locomotor activity (see 4-2.2). It is likely therefore that the high incidence of feeding movements observed during the first segment of a fight is a consequence of the starved crabs being introduced to an environment containing olfactory cues.

Figure 4.42 also suggests that Pattern 17 (striking an opponent) is bi-model in its distribution with peak occurrence during the third/fourth segments and the seventh/eighth segments. This is shown for winners, losers and responders, however, the trend is less marked for initiators.

The data presented for Pattern 18 (grasping an opponent) (Figure 4.42) shows a number of interesting features. This behaviour pattern was shown mainly by winning crabs and mainly by crabs which did not initiate an interaction. In addition the plateau region shown during the fourth-eighth segments probably reflects the nature of the

behaviour pattern. That is, grasping usually occurs during the first two or three segments of a fight in response to an initial approach from an opponent. This accounts for the sharp increase observed during the first two or three segments in the plot for winners and responders. Once initiated, a grasp was often held for a considerable period of time before release of the opponent which usually then withdrew rapidly.

These results (Figure 4.42) therefore, indicate that some system-atic trends occur within interactions but that these trends are only observed from some of the behaviour patterns studied. However, the results emphasise one other interesting point. The distribution of behaviour patterns across an interaction (i.e., the shape of the plots in Figure 4.42) are remarkably similar for winning and losing crabs. The same is true for initiating and responding crabs, and this appears to agree with the data presented in section 4-3.5 that both interactants within an interaction show very similar behaviour patterns. ✱

4-3.8 THE ORGANISATIONAL RELATIONSHIP BETWEEN PATTERNS IN A FIGHT

Results and discussion concerning the organisational relationship between patterns in a fight are presented in Appendix D. These results are presented separately due to their inconclusive nature.

Figure 4.42

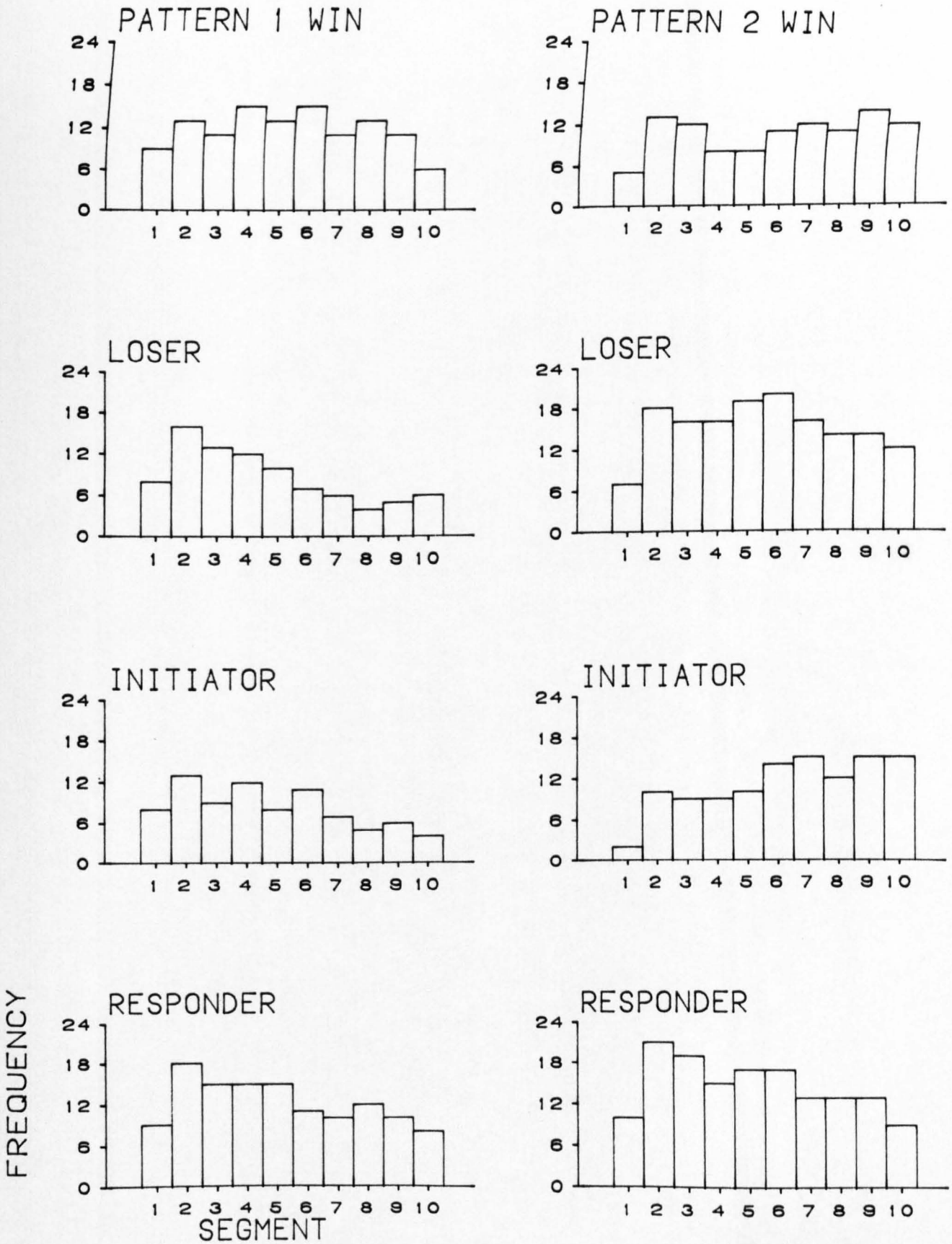

PATTERN 1 WIN
PATTERN 2 WIN
LOSER
LOSER
INITIATOR
INITIATOR
RESPONDER
RESPONDER
FREQUENCY
SEGMENT
0
6
12
18
24
1 2 3 4 5 6 7 8 9 10

Figure 4.42 contd.

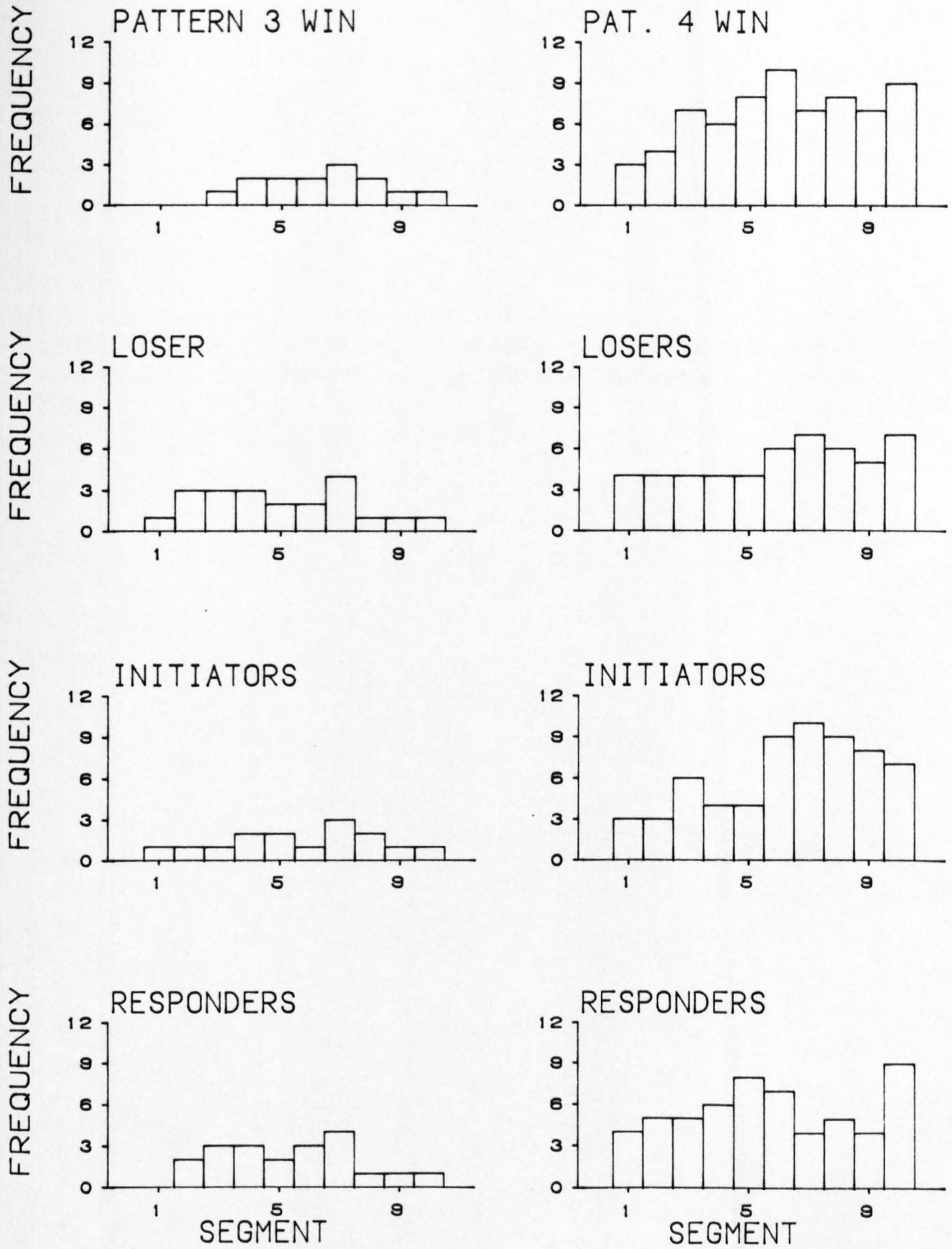


Figure 4.42 contd.

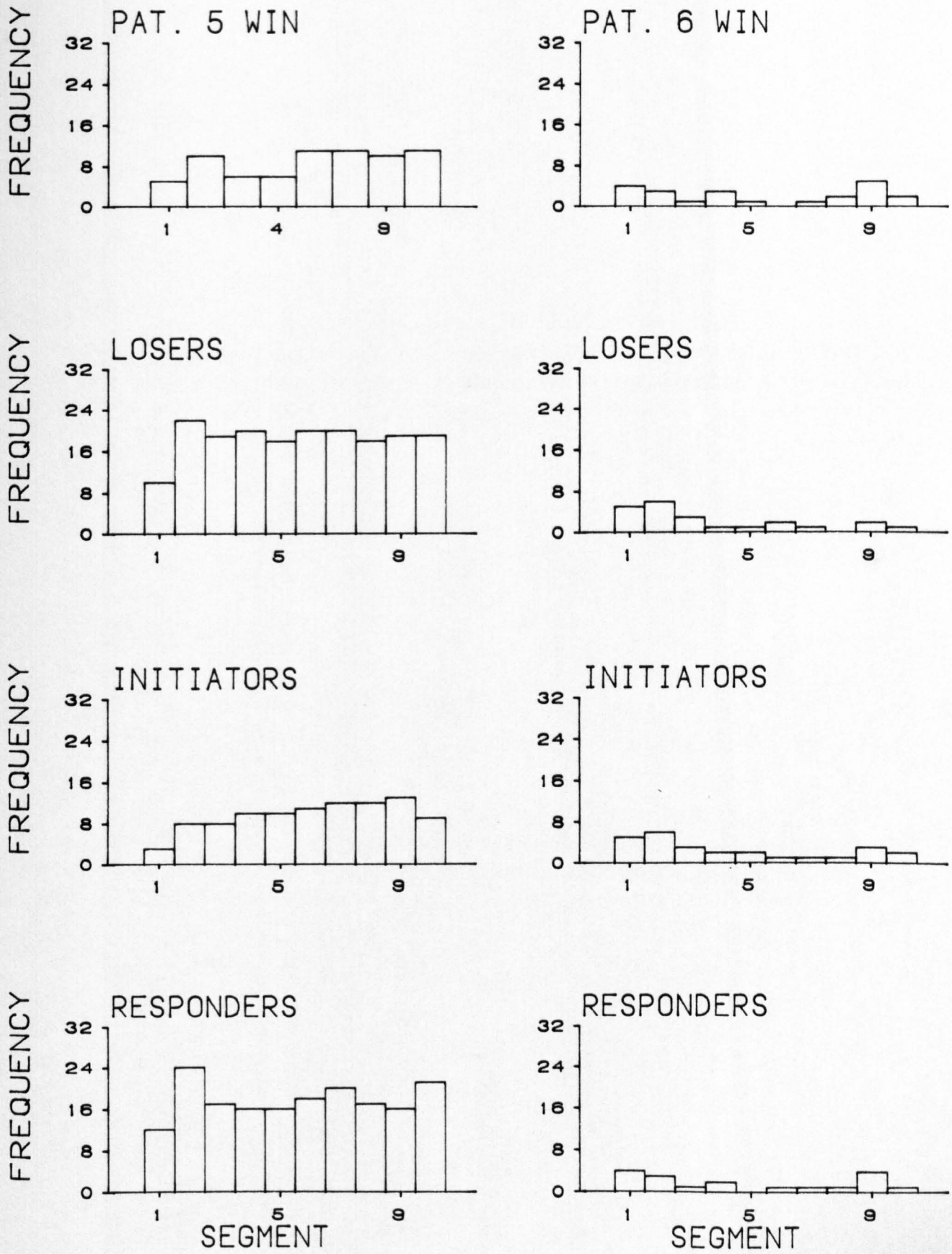


Figure 4.42 contd.

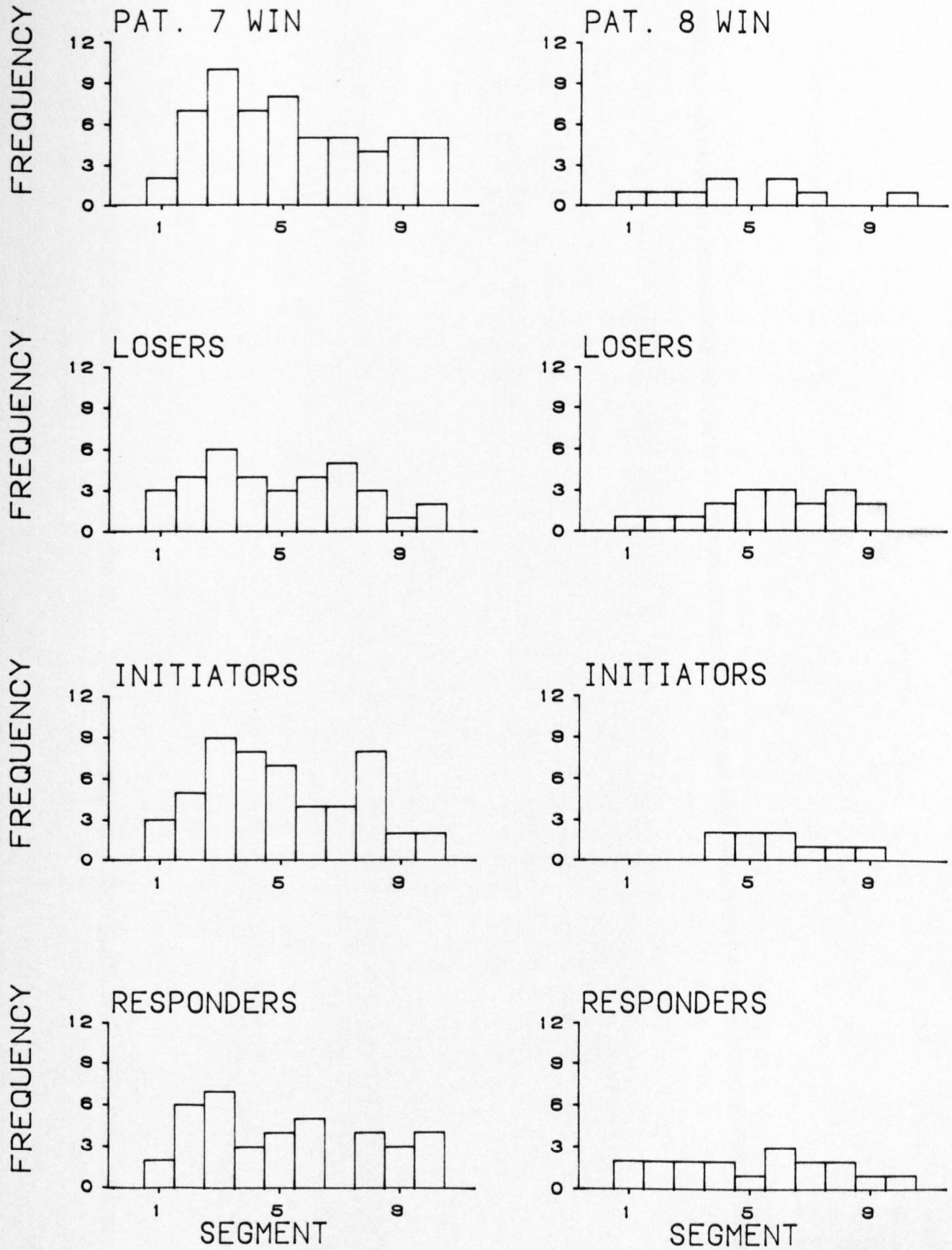


Figure 4.42 contd.

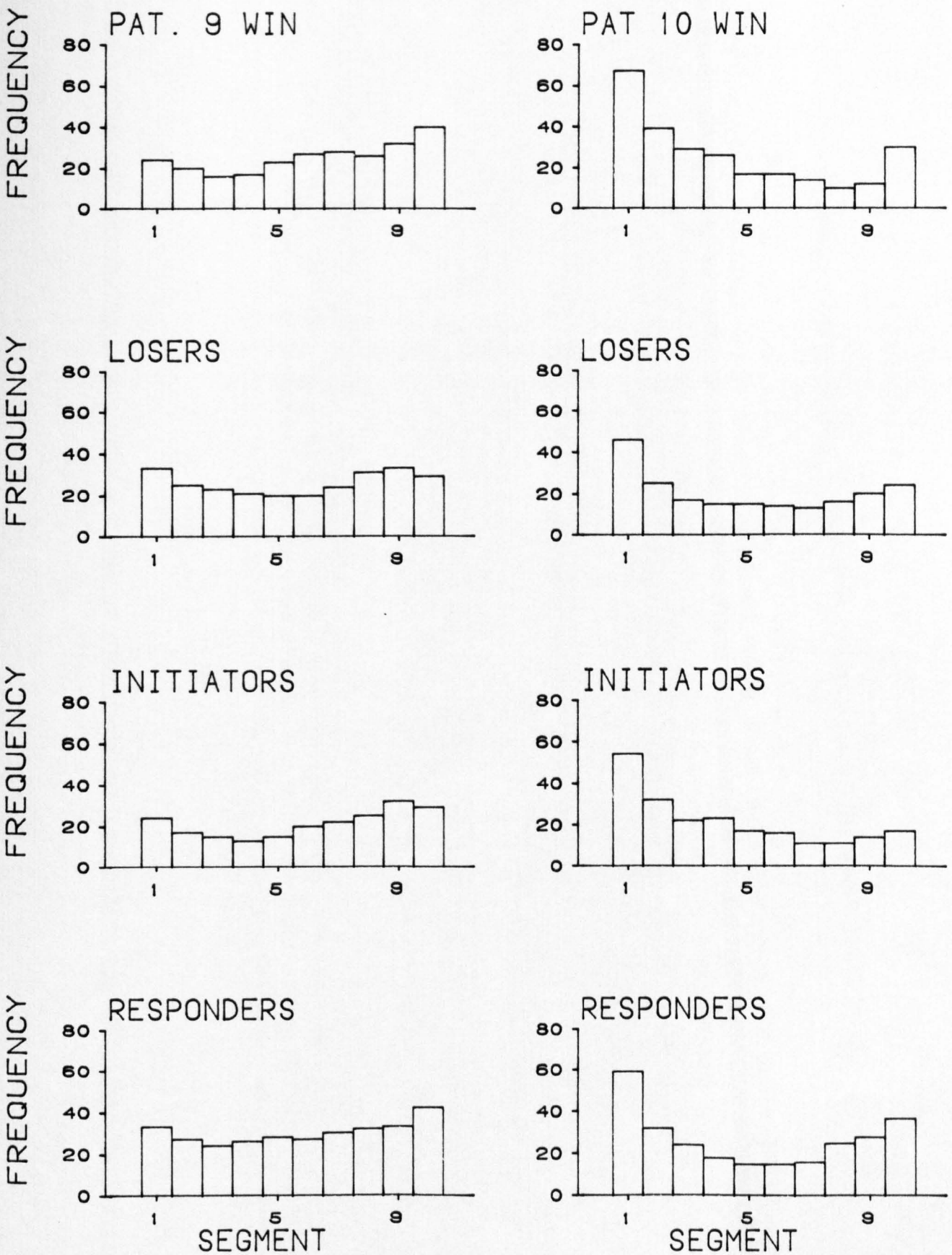


Figure 4.42 contd.

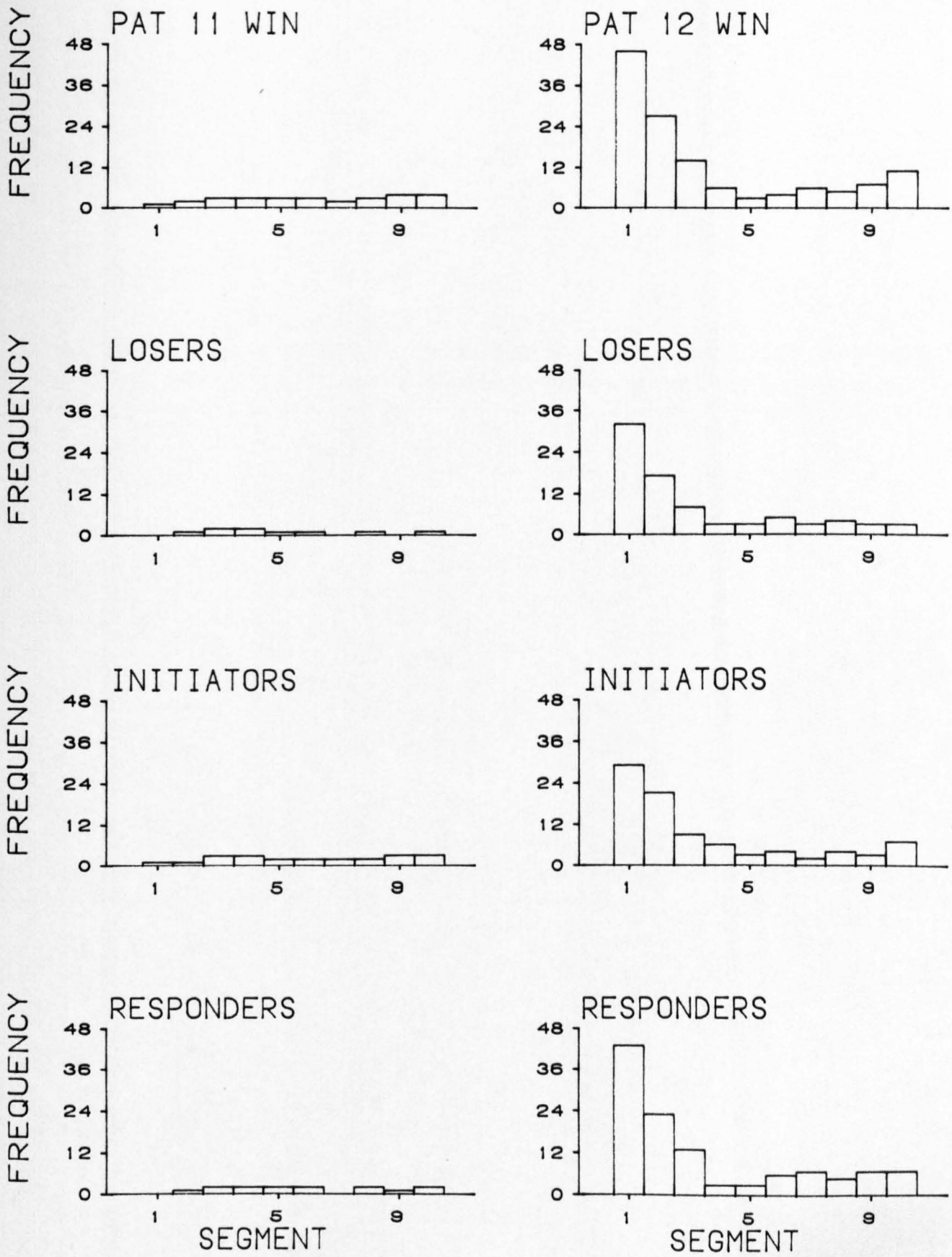


Figure 4.42 contd.

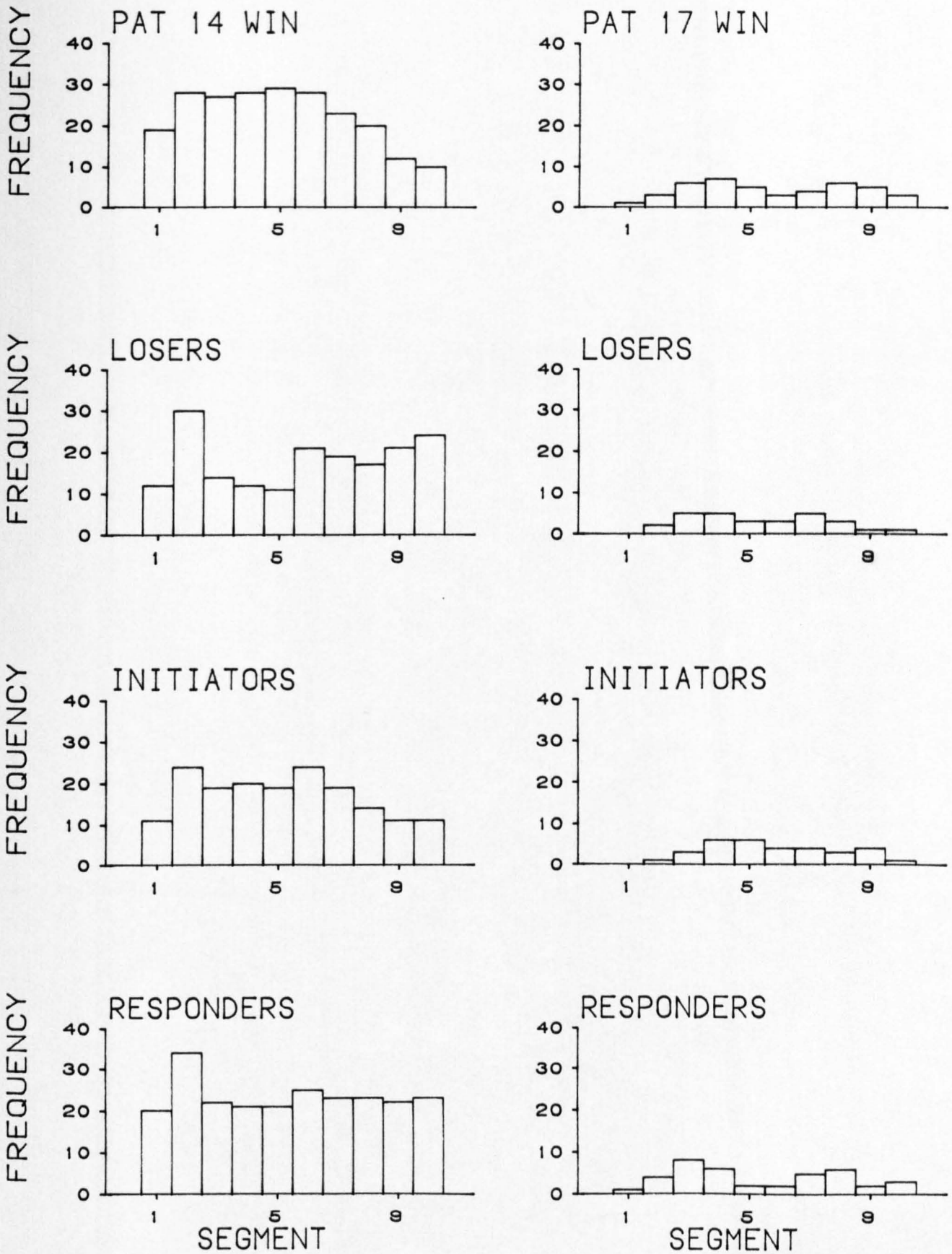
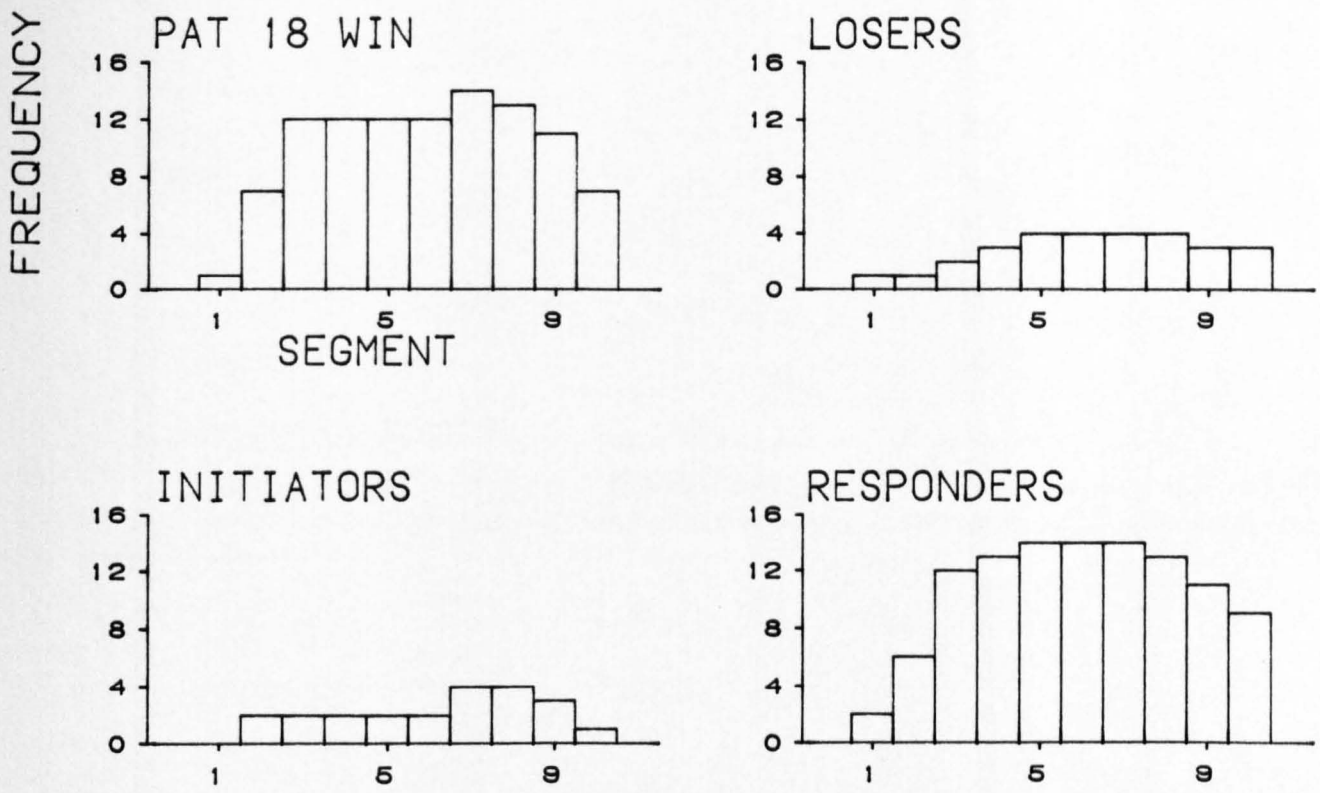


Figure 4.42 contd.



4-4 DISCUSSION

The major aims of this study were:-

1. To characterise the movements and postures and the normal course of events in a fight between male crabs; to relate this to the behaviour shown in the field and to make deductions concerning the mechanisms controlling the behaviour.

2. To examine any behavioural differences shown between winners and losers and initiators/responders.

3. To investigate the effects of size on the initiation, form and outcome of interactions.

4. To investigate the possibility that consistent individual differences in style of aggressive behaviour exist.

The intention, in this section, is to take each point in turn but the nature of the data is such that this may not always be possible.

4-4.1 QUALITATIVE DESCRIPTION OF AGONISTIC BEHAVIOUR

Extensive preliminary observations indicated that the behaviour of L. depurator may be broken down into a number of discrete units. With

other crustacean species, such as hermit crabs, the units of behaviour are simple and easily observable. With L. depurator the units are of a more complex nature but none the less definable.

In fights between male L. depurator, after orientation towards one another, both crabs assume one or other of the postures outlined in section 4-3. This usually involves raising the body from the substrate, extending the walking legs and stretching the chelipeds towards the opponent with the chelae held in the open position. In addition, the fourth pair of walking legs or fifth pereiopods are raised and extended over the carapace. This behaviour shown in the presence of another crab is quite different from that shown by isolated crabs (see section 4-3.2).

Many other brachyurans show this raising of the body and extension of the chelipeds but L. depurator differs in that the fifth pereiopods are also raised and extended. The raising of one or more walking legs during agonistic encounters, is common (Warner, 1977) but rarely involves the last pair of legs. In the frontal approach commonly used by hermit crabs and spider crabs a pair of legs (usually the 2nd and 3rd walking legs) may be raised together, which presents to the recipient a dramatic cross shaped posture (Hazlett, 1972a, b). In crabs which approach sideways, the raised leg is usually directed towards the other crab and similarly the 2nd and 3rd walking leg is used. This occurs in the European hairy crab, Pilumnus hirtellus (Lobb, 1972) and in the mangrove crab, Goniopsis, (Warner, 1970). In L. depurator, the 2nd-4th pairs of walking legs are not raised from the substrate at any point in an interaction. However, the swimming legs are raised and due to the flattened nature of the dactylus or

paddle which is held face on to an opponent, a dramatic increase in frontal area and hence visual size is obtained.

This type of posture is unique to the swimming crabs. Lobb (1972) suggested that leg raise postures may have arisen by evolution from an exploratory movement performed as a prelude to locomotion. This may also help to explain the use of swimming legs rather than ambulatory legs by L. depurator. When disturbed, L. depurator runs rapidly across the substrate while waving its swimming legs backwards and forwards over the carapace, movements which are characteristic of swimming in brachyuran crabs (Hartnoll, 1971). It is quite possible therefore that the swimming legs provide extra propulsion, thereby enabling the crab to move more quickly over the substrate than running alone would permit. If this is the case, then raising the swimming legs in readiness for escape when faced with a novel stimulus may have considerable adaptive significance. It is possible therefore that the swimming leg raise posture shown by L. depurator has arisen from movements performed in readiness for rapid locomotion just as ambulatory leg raise has in other crabs (Lobb, 1972).

After initial orientation, four distinct types of fight may be observed in L. depurator interactions. These include stationary displays (Category 1), single approach/retreat interactions (Category 2), interactions involving multiple approach/retreat before conclusion (Category 3), and fights involving physical contact between interactants (Category 4), categories 2 and 4 being the most common (Table 4.3a)

Fights settled without any ambulatory movement prior to final retreat by one individual (Category 1) are rare in the literature on crustacean behaviour. However, this may simply reflect the fact that most other studies (Hazlett, 1966a; Hyatt, Smith and Raghavan, 1979; Elwood and Glass, 1981), consider an encounter to have started only after an approach. That it occurs in L. depurator implies that the crabs are sometines able to assess each other from a distance and where appropriate, withdraw without any further interaction. It is quite likely that the same may be true for a number of other crustacean species but that this has not become evident due to the definition concerning the beginning of an interaction.

Interactions in many species are settled without any physical contact (Warner, 1970; Hazlett, 1972a, b) but in every instance, some form of initial ambulatory approach is made by one or other of the interactants. For most interactions, in L. depurator, only one approach is sufficient to settle the fight but in others (9%) multiple bouts of approaching and retreating are required before termination. This again may be a matter of definition. Most studies on crustacean behaviour define the completion of an interaction as retreat by one individual even if this retreat is in the face of an approach by the other interactant. Under these conditions, an interaction may continue but this will not be recorded. The present study and that of Elwood and Glass (1981) on hermit crabs, both show multiple approach/retreat categories as by definition, interactions terminate only on retreat of one animal from a stationary opponent. It is quite likely therefore that multiple approach/retreat interactions may be rare in the literature, due to the experimental definitions.

Over 39% of all fights observed in L. depurator involved physical aggression in the form of striking or grasping an opponent. In crustaceans, it has been reported that fights are usually settled by a mutual exchange of signals and associated advances or retreats. As more studies are published, however, it is becoming apparent that physical contact may be more common than previously accepted. Touching the other crab with a walking leg or the tip of a chela (Vannini and Sardini, 1971; Lobb, 1972) is quite common; Goniopsis push against each other using the outer faces of the chelae in a shield position; Aratus pushes against an opponent with interlocked chelae in the outstretched position (Warner, 1970); Pilumnus (Lobb, 1972) and the Italian river crab Potaman fluviatile (Vannini and Sardini, 1971) use both pushing and grasping, while striking with the tips of the chelae is seen in Potamon, Callinectes (Jackowski, 1974) and Goniopsis. In addition, Elwood and Glass (1981) reported that physical contact was shown frequently during hermit crab shell fighting. Physical aggression in the crustacea therefore, has been shown to exist in a wide number of groups and species, but with the exception of the results presented by Elwood and Glass (1981), physical contact usually only occurs between evenly matched individuals.

The results of the current study show that physical contact is common during interactions between male L. depurator in the laboratory and this is in general agreement with some previous reports on crustacean behaviour. However, the behaviour of L. depurator differs from that reported for other species in that physical aggression is not restricted to closely matched pairs.

The mean SDI value for type 4 fights lies between that for types 1 and 2 (Table 4.3a) and pairs of crabs with an SDI of as much as 0.40 may become involved in physical aggression. In addition, it is not always the larger of the two crabs that performs the physical contact.

Although physical contact may be more common among the crustacea than previously reported, the levels of physical aggression observed in this study (39% of all fights) is higher than that reported for other studies. There are a number of possible explanations for this high observed rate of aggression.

1. It may be an artefact brought about by the experimental design. L. depurator is a highly active animal and it is possible that confining two crabs in a small experimental tank may result in high levels of physical contact though many other species were studied in the laboratory without such high levels of aggression. However, Jackowski (1974) in a laboratory study on the swimming crab Callinectes also reports quite high levels of physical contact.

2. L. depurator may naturally be a highly aggressive animal, although field studies (Chapter 2) do not seem to support this.

3. The presence of an olfactory stimulus to a food deprived animal may induce higher levels of physical aggression than may otherwise be expected.

It is quite likely however, that a combination of all three possibilities is involved.

Within the fights themselves, the flow diagrams of the main sequence of events (Figures 4.23 and 4.24) reveal a number of differences between the crab that initiates an encounter and that which responds, and also between winners and losers. Very few differences were found between eventual winners and losers in the overall frequency of the different acts (Table 4.3b) but some subtle differences did exist within the sequence of behaviour shown.

After a period of stationary display, crabs which eventually won were more likely to approach an opponent than those which eventually lost an encounter. In addition, during multiple approach/retreat encounters, no winning crab was observed to revert from a stationary display to a retreating display, while this was observed frequently for losing crabs. Other differences were observed in the incidence of striking and grasping an opponent. Winning crabs were more likely to strike and to grasp their opponents than were losing crabs. This is further emphasised by the observation that during approach to another crab, both striking and grasping were more frequently shown by the ultimate winner. Thus at some point before the end of an interaction, behavioural differences between the ultimate winner and loser of the encounter are evident. The analysis of change of behaviour during the course of an interaction (4-3.4) indicates that these differences may be manifest from early stages in a fight. One possible explanation for this is that during a stationary display, each crab is carrying out some form of assessment of its opponent and as a result of this assessment a conclusion may be reached.

As is the case for winners and losers, some differences between initiators and responders are evident in terms of the overall flow of behaviour patterns. Initiators are more likely than responders to transfer from a stationary display to an approaching display. This is in good agreement with the results for winners/losers, however, the incidence of striking or grasping an opponent is not significantly different for initiators/responders unlike that already shown for winners/lossers.

Comparison of the overall sequencing of events (Figure 4.23 - 4.26) shows that there are sufficient differences to suggest that the behaviour shown by winners is not necessarily the same as that for initiators, and similarly for losers/responders. This is in contrast with the results presented by Hazlett (1966b), Vannini and Sardini (1971), Lobb (1972) and Rubenstein and Hazlett (1974) where initiators were normally the winners of interactions. A full discussion of this is given in section 4-4.2.

4-4.2 DETERMINANTS OF INITIATION AND OUTCOME OF INTERACTIONS

Although larger crabs win most fights, smaller crabs are also capable of winning, especially when difference in size between opponents is small. This agrees with the results presented by Elwood and Glass (1981) where winning in hermit crab shell fighting was not restricted to the larger interactant but where smaller crabs only won if the size differential was small. Why is it sometimes possible for the smaller crab to win?

One possible explanation is that the assessment procedure being carried out is not particularly reliable and that this effect is most pronounced where the size differential is small. An alternative explanation is that motivational differences may be important. In the laboratory only those crabs in inter-moult condition were used. In the wild, not all crabs will be in this condition and the motivational state of a crab may change immediately prior to and immediately after moulting. Under these circumstances, all crabs would not be expected to react in the same or any consistent manner. In addition, many other internal factors with no outward signs such as hunger, parasitism, disease may greatly modify the behaviour of an animal. Therefore, even though a crab appears large to its opponent, there may be few outward signs of how hard the crab might fight for the resource in dispute.

Since larger crabs generally win fights against smaller conspecifics, arguments from a games theory perspective suggest that larger crabs should initiate encounters (Maynard-Smith and Parker, 1976) and smaller crabs should not initiate fights as they are likely to loose. Several studies (Hazlett, 1968; Vannini and Sardini, 1971; Lobb, 1972; Rubenstein and Hazlett, 1974) provide support for this prediction, showing that approaching and initiating is much more commonly observed in larger crabs, which will normally win (Warner, 1977).

The present study indicates that this is not the case for L. depurator. In addition, Jackowski (1974) reported similar results for the swimming crab Callinectes sapidus where small crabs initiated interactions as frequently as did large crabs. Why then, for

swimming crabs at least, are smaller crabs just as likely to initiate an encounter as larger crabs? There are a number of possible explanations.

1. Assessment may not be possible at an early stage. Assessment of the size of an opponent may be impossible (or at least difficult) unless the animals concerned are orientated towards one another and raised from the substrate indicating clearly their actual size. In other words, a crab may not be aware that it is smaller than its opponent until an interaction has been initiated.

2. Assessment of RHP may not be easy. If size differential is small, or if other invisible factors such as motivational state are important, rapid assessment of relative RHP may be difficult, hence interactions may be initiated by any crab irrespective of relative size.

3. The benefits associated with the small chance of winning, allied with the small costs of losing an encounter, may make it acceptable for a small crab to engage in a fight.

As with the case of the high observed incidence of physical contact (4-4.1) it is quite likely that some combination of all three of these possibilities may be responsible for the fact that small crabs are just as likely as large crabs to initiate fights.

4-4.3 INTERACTION LENGTH

Interactions are very variable in length ranging from eight frames to 266 frames with a mean fight length of 48 frames or 24 seconds. These fights are in general longer than those reported for most other crustacean species where fights are described as brief, though few studies have attempted to measure fight length systemmatically. Crane (1967) reported that in Uca, bouts of up to 3 minutes were recorded. Hazlett (1971) reported that aggressive encounters among three species of Hawaiian portunids were also brief (a few seconds) as did Jackowski (1974) in a study on the portunid Callinectes. Notable exceptions to this rule of brief fight length in the crustacea are hermit crabs fighting over shells which are often in short supply, and some species of stomatopod as reported by Dingle (1983). Fights of up to 20 minutes in length were reported by Elwood and Glass (1981) for Pagurus bernhardus while contests of 10 minutes were reported by Dingle (1983) for the stomatopod Gonodactylus chiragra. The latter may however be a direct consequence of the experimental procedure where animals were held in open arena contests and allowed to interact for a period of 10 minutes.

The cumulative distribution of fight lengths, except for under representation of very short fights, follows the negative exponential curve. At a first glance this appears to support the War of Attrition model. This model represents a contest which is settled by display alone, and individuals are imagined to show their display at constant intensity until one gives up leaving the other, which was prepared to go on at this point, the winner. Maynard-Smith (1974) showed that the ESS is to choose the duration of the display according to the

negative exponential. In his analysis, Maynard-Smith assumed that the cost of display would be a linear function of its duration although Caryl (1981) states that this assumption may not be valid or necessary, and that the model can be extended (Bishop and Cannings, 1978) in terms of a 'cost function' that relates the cost of the display to its duration. It is possible therefore to explain the distribution of fight lengths shown in this study, in terms of this simple model. That is, animals display for a given duration before giving up. However, this does not take into consideration the fact that fights were not necessarily between evenly matched crabs (i.e., asymmetry in RHP exists). Further examination of the results shows that there is a tendency for interactants with a small SDI (closely matched crabs) to interact for longer than pairs in which the SDI is large.

This situation is further complicated (Table 4.6) as absolute size also has a bearing on interaction length. Fights between two large size class crabs (L x L) are significantly longer than those of any category other than M x M fights. In addition, multiple regression analysis shows that the absolute size of the smaller crab in a pairing is the most important factor affecting fight length. The effect of the size of the larger crab (the second largest predictor) on fight length is not significant.

It seems therefore that fight length is a function of the size of the opponents, so that the assumptions of the War of Attrition model are violated. Pairs of crabs with a small SDI fight for longer than pairs with a large SDI while closely matched large crabs fight for longer than closely matched small crabs. Why should closely matched large crabs fight for longer than closely matched small crabs? It seems

unlikely that energetic constraints are important. All crabs used were adult crabs with no outward signs of disease or illness, and there is no evidence in the literature to suggest that smaller crabs are physically or energetically constrained in their behaviour.

An alternative explanation is that smaller crabs are less hungry than large crabs. This also seems unlikely, as even though each crab was fed an identical amount of food between interactions irrespective of the size of the crab, the food was sufficient to allow the crabs to feed to satiation, with uneaten food being removed from the experimental tank 24 hours after introduction.

Hazlett (personal communication) suggests that the difference in behaviour shown by different populations of Pagurus bernhardus (Hazlett, 1978; Elwood & Glass, 1981) are a consequence of inexperience on the part of the population of young crabs studied by Elwood and Glass. This is disputed by Elwood and Glass and evidence now exists to show that the behavioural repertoire of young (small) P. bernhardus is identical to that of older (larger) crabs, at least for a population of crabs on the North Down coast, N. Ireland (Elwood, MacClean; pers. comm.). It seems unlikely therefore that inexperience on the part of the smaller crabs in the current study is responsible for the observed difference in fight lengths.

The results of the field investigation (Chapter 2) indicate that almost all matings are carried out by the largest male crabs; small male crabs are physically incapable of holding receptive female crabs in a mating clasp. If fights are over females, then in the field, as a male crab gets larger, the benefits of winning an interaction may increase

(where the benefit is a greater chance of mating). Although interactions in the laboratory were induced by olfactory feeding stimuli and not induced by the presence of a receptive female, it is possible that the aggressive system is primarily adapted for competition over females. Larger crabs may therefore be prepared to fight for longer as, in the field at least, the benefits of winning may be greater to a larger crab than to a smaller crab.

None of these explanations satisfactorily explains the observed variation in fight length and it is obvious that further laboratory studies are necessary in order to identify the true causal relationship.

4-4.4 CHANGE IN BEHAVIOUR DURING THE COURSE OF AN INTERACTION

Many animal species show a progressive quality of changes in behaviour during the course of a fight (Caryl, 1981). This concept of a series of behaviour patterns revealing gradually increasing levels of aggressiveness is an idealisation, but even so, the progressive changes in the duration or frequency of behaviour patterns in the interaction are loosely compatible with the idea that combatants may become progressively more aggressive until one gives up.

The fight profiles presented in section 4-3.7 indicate quite clearly that when L. depurator fights are divided into segments there is no evidence to suggest that such a pattern of escalation occurs in any of the categories studied. The behaviour patterns discussed, appear to

occur with equal frequency in all segments of a fight and those trends which do occur tend to reflect arbitrary distinctions concerning the beginning and end of an interaction.

4-4.5 COMPARISON OF BEHAVIOUR SHOWN BY INDIVIDUAL CRABS FROM INTERACTION TO INTERACTION.

The multiple interactions studied in section 4-3.5 were investigated to see whether individual crabs showed any consistent style of aggressive behaviour in terms of individual behaviour items. Figures 4.31 - 4.41 indicate that the majority of fights follow a set pattern although there may be a certain amount of variability around this general plan. The standard plan is for both crabs to start at Pattern 9 or 10, to move up to Pattern 1 or 2 and then revert to Pattern 9 or 10 at the end of the fight after moving through various other patterns. These profiles show no evidence of progressive increase in intensity of display over the course of a fight so the concept of escalation is not useful for this species. However, the results do show that within any given interaction, both crabs show very similar behaviour patterns (i.e., they match each other) irrespective of their SDI or the final outcome of the interaction. These results indicate that L. depurator shows general consistency in style of aggression rather than individual and unique consistency.

Section 4-4.2 discussed how uncertainty about relative RHP and fighting motivation may result in competing crabs requiring to engage in some form of behavioural interaction. It is now necessary

to discuss why they use many different behaviour patterns and why they appear to match the behaviour to that of the opponent. In species where escalation is a valid concept such as the Siamese fighting fish Betta splendens (Simpson, 1968) and the killifish Aphyosemion (Dow et al., 1976) different behavioural acts are sufficient to allow a process analagous to bidding at an auction (Simpson, 1968) with each interactant trying to match or outbid the opponent. In L. depurator however, fights do not follow a plan of progressive escalation so this explanation cannot apply even if it is valid in other cases.

It is difficult to put forward an alternative explanation for this matching behaviour but one possibility is that the matching process enables a crab to estimate the relative RHP more easily than would be possible otherwise and that this system functions most effectively if both crabs adopt identical behaviour patterns.

4-4.6 ORGANISATION OF BEHAVIOUR WITHIN AN INTERACTION

The results of section 4-3.5 indicate that within a given interaction, the behaviour of one crab matches closely that of the other. Under these circumstances few differences in overall organisation should be observed between winners and losers or between initiators and responders. It is possible, however, that differences may occur between fights of different lengths with different proportions of the various behaviour patterns being shown. The results presented in section 4-3.6 show the comparisons made between fights of different

lengths and also with the different length fights split into winning, losing, initiating and responding categories.

It is quite clear from these results that very few differences, in the proportion of behaviour patterns shown, exist between any of the categories examined. Any differences which do exist are minor, the implication being that whether fights are long, short or intermediate in length the balance of frequencies of different behaviour patterns within a fight is very similar.

4-4.7 CONCLUSION

The results presented in this chapter indicate that L. depurator is a highly aggressive animal readily interacting with conspecifics, and also that physical contact occurs in a high percentage of fights (39%). The results presented in Chapter 2 however, indicate that although L. depurator is found clumped together, the incidence of aggression in the field is low and that physical contact is extremely rare or non-existent. This raises the possibility either that the patterns of behaviour described in this section are laboratory artefacts or that the results of the field surveys do not adequately reflect all aspects of the behaviour of L. depurator.

L. depurator is a very active animal both in the field and in the laboratory, and it is likely that confinement in a small tank may induce a higher than normal incidence of aggression. This is further emphasised by the fact that crabs were often found in dense groups (5 crabs/m^2) in the wild with no evidence of aggression of any

description. In addition, on a number of occasions, dense groups of crabs were observed in which one individual was observed in possession of a food item, without any aggravation from the conspecifics.

However, it is clear that the increased levels of aggression shown in the laboratory are not a complete artefact. Other active species, when housed in similar experimental tanks do not fight as readily as L. depurator does. In addition, agonistic encounters, triggered by a passing diver were actually observed quite commonly in the field (see section 2). This indicates that crabs in the wild are capable of showing the full repertoire of behaviour patterns shown in the laboratory, but that under the conditions met at the study sites, only part of the full repertoire was shown. It is quite likely that under different conditions of population density, food availability or predation level in the field, different populations of crabs may be able to show varying degrees of the full behavioural repertoire available.

Assuming that the fights in the laboratory are a valid extension of the behaviour patterns shown in the field, what are the fights really about? It is clear that size of interactants is a major factor influencing both outcome and duration of a contest. However, it is equally clear that size is not the only factor concerned. Assessment both of other aspects of RHP and of motivational state must also be carried out in order that a conclusion may be reached. It appears that each crab matches or mimics the behaviour of the opponent during this assessment procedure, and perhaps this matching behaviour enables a reliable estimate of relative RHP and

motivational state to be achieved. It is likely that, as with other species, this complex repertoire of agonistic behaviour in L. depurator probably allows encounters to be decided with a minimum of costly high intensity fighting.

4-5 SUMMARY

1. 107 paired inter-male interactions, carried out in a round-robin series between 47 individual crabs were recorded on videotape from which a qualitative description of the agonistic behaviour of L. depurator was obtained.

2. Flow diagrams of the main sequence of events were prepared for initiators, responders, eventual winners and eventual losers. Few differences were observed in the overall pattern of these flow diagrams.

3. Four main categories of interaction were observed and the incidence of each discussed. The four categories were, fights settled by stationary display; fights settled by a single approach/retreat; fights involving multiple bouts of approach/ retreat; fights involving physical contact between contestants.

4. Behaviour patterns were described for a number of isolated individuals and compared with the behaviour shown by interacting pairs of crabs. The behaviour shown by single crabs was markedly different from that of paired interactants.

5. Determinants of the initiation and outcome of interactions were discussed. Small crabs were just as likely to initiate an interaction as large crabs and there was no significant difference between initiators and responders in terms of winning or losing an interaction.

6. Smaller crabs were capable of winning interactions but only when size difference between individuals was small.

7. Interactions ranged from eight frames up to 266 frames in length with fights between large size class crabs lasting longer than fights of any other category. The size of the smaller crab was shown to be the most important factor affecting fight length.

8. Comparison of behaviour shown by individual crabs from interaction to interaction showed that the majority of fights followed a set pattern and that within any given interaction, both crabs showed very similar behaviour patterns irrespective of the SDI or the final outcome of the interaction. The implications of this matching behaviour were discussed.

9. Comparisons made between fights of different lengths and also with the different length fights split into winning, losing, initiating and responding categories showed that very few differences existed in the proportion of behaviour patterns shown in any of the categories examined. The differences which did exist were minor and did not reflect major differences in organisation between the different categories.

10. When fights were divided into segments there was no evidence to suggest that progressive escalation in intensity occurred in any of the categories studied. The behaviour patterns occurred evenly over all segments of a fight and those trends which did exist tended to reflect arbitrary distinctions concerning the beginning and the end of an interaction.

CHAPTER 5

GENERAL DISCUSSION

The main aim of this study was to attempt to fill in some of the gaps in our knowledge of the biology of L. depurator by a series of closely related laboratory and field studies.

Field studies were carried out at Loch Sween (Argyllshire) in an attempt to describe the behaviour and ecology of L. depurator as a background for subsequent laboratory studies. Abundance of animals varied over time at the study site with peak abundance corresponding with periods of warm water (September-November). During these periods of peak abundance, densities of 1 crab /7m^2 were observed, but average density was much lower at 1 crab/25m^2. Some evidence for migration from the study site similar to that for other species was observed but further tracking studies will be necessary in order to elucidate the movement patterns of individuals. Individuals within the study area were continually changing even though in the short term, local abundance remained relatively constant. Summer populations were shown to be biased in favour of male crabs but extensive transect surveys failed to identify differential male/female migration again exposing the need for further tracking studies. Individuals were most commonly observed within 1 metre of the nearest conspecific and localised densities of up to 3.3 crabs/m^2 were reported. These local aggregations did not appear to be formed by single sex groups.

Ovigerous crabs were observed in two distinct phases between April and September and this observed brooding period is substantially different from that reported in some studies. This discrepancy probably highlights an inadequacy in the sampling of certain areas

and suggests that the brooding period of L. depurator may be longer than previously stated. As far as recruitment is concerned, this occurs in early spring, but the observed subsequent increase in adult crabs is caused by movement of large crabs into the study area, not by growth and maturation of the early spring immigrants.

Habitat utilisation was non-random and possibly associated with feeding and anti-predator behaviour. Observations on food and feeding behaviour showed L. depurator to be predators of sessile or slow moving benthic macroinvertebrates with the ability to capture larger, fast moving prey if the opportunity arises. Three main types of antipredator response were identified and discussed, as was the incidence and possible causes of physical damage shown by the crabs. Levels of physical damage in the field were lower than those observed in laboratory populations, probably due to lower density of crabs in the field. A number of naturally occurring social interactions were observed in the field. These were described and the results provided a basis for the study of aggressive interactions in the laboratory. The observed incidence of such aggression in the field was very low.

This field study not only presents information on the ecology and habitat utilisation of L. depurator, it provides a description of the behaviour of this species under natural conditions. In addition, it also fills part of the gap left by the fisheries orientated approach and provides the background information necessary for subsequent laboratory studies.

Furthermore, as well as providing a background account, the present study provides valuable comparative information which may have implications for the study of other important species.

Subsequent to the field study, further experiments were carried out in the laboratory to provide important information for the planning of other experiments and to answer questions concerning the locomotor rhythmicity of L. depurator. Locomotor activity of 34 individual swimming crabs from one shallow water and one deep water site, was studied using autocorrelation and Fourier transformation in order to detect any rhythmicity present in the time series data. Significant rhythmicity was displayed under all three lighting regimes employed (LD 12:12; LD 24:0; LD 0:24) indicating that activity was not induced by the cyclic laboratory environment.

Shallow water crabs displayed significant cyclic locomotor activity while deep water crabs displayed arhythmic activity. A predominant 25 hour cycle was displayed by the shallow water crabs in which peak activity corresponded with 'expected' night time flood/high tide. This pattern of activity may be an adaptation to life in a cyclic environment allowing efficient foraging without a greatly increased risk of predation. In light of these experiments, it was decided to employ only arhythmic (deep water) crabs in all subsequent experiments in an attempt to reduce variables.

Further laboratory studies were carried out whose major aims were to characterise the movements, postures and normal course of events in fighting between male crabs; to relate this to the behaviour shown in the field; to investigate the possibility of consistent individual

differences in style of aggressive behaviour; to investigate the effects of size on the initiation, form and outcome of interactions; to examine behavioural differences shown between winners and losers.

A full description of the agonistic behaviour of L. depurator was obtained and examination of flow diagrams of the main sequence of events in a fight showed that few differences existed in the overall pattern for eventual winners, eventual losers, initiators and responders. However, investigation of the determinants of initiating interactions and of the outcome, revealed that small crabs were just as likely to initiate an interaction as large crabs and there was no significant difference between initiators and responders in terms of winning or losing an interaction. Smaller crabs were also capable of winning interactions, but only where SDI was small.

L. depurator is an important member of many sub-littoral communities. As such, it is surprising that prior to this study little attention has been paid to the general biology, ecology and behaviour of the animal. This study has attempted to describe the ecology and behaviour of the animal both in the field and the laboratory. Although much more work is required before the biology of L. depurator is fully understood, this study forms a detailed base line upon which further work of both a comparative and specific nature may be based.

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APPENDIX A

Sample data file obtained from locomotor activity experiment.

Filename = CWGD07.DAT

No. of data points = 256

Start of data gap = 0

Length of data gap = 0

Start time of expt. = 13 0

Initial light state = 1

Interval numbers of changes in light state:

12 36 60 84 108 132 156 180 204 228

Sex = 1

Carapace length = 35

Carapace width = 47

Experimental identification:

LD 12:12

Int.No.	Ch.1	Ch.2	Ch.3	Ch.4	Ch.5	Ch.6	Ch.0
1	25	18	7	9	18	25	102
2	0	0	0	0	0	0	0
3	25	0	0	0	0	0	25
4	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0
13	8	0	0	0	0	0	8
14	8	0	0	0	0	0	8
15	19	0	0	0	0	0	19
16	155	0	0	0	0	0	155
17	12	8	3	7	9	15	54
18	9	4	3	5	2	21	44
19	14	10	0	0	0	0	24
20	1	0	0	0	0	0	1
21	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0

25	0	0	0	0	0	0	0
26	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0
31	1	0	0	0	0	0	1
32	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0
34	36	8	12	9	7	68	140
35	30	18	22	24	19	107	220
36	5	6	4	1	2	136	154
37	21	26	14	9	11	100	181
38	0	4	2	3	1	39	49
39	0	0	0	0	0	0	0
40	0	0	0	0	0	31	31
41	0	0	0	0	0	0	0
42	0	0	0	0	0	0	0
43	0	0	0	0	0	0	0
44	0	0	0	0	0	0	0
45	17	4	2	3	9	17	52
46	4	2	1	3	5	7	22
47	0	0	0	0	0	0	0
48	0	0	0	0	0	0	0
49	0	0	0	0	0	0	0
50	0	0	0	0	0	0	0
51	0	0	0	0	0	0	0
52	0	0	0	0	0	0	0
53	0	0	0	0	0	0	0
54	0	0	0	0	0	0	0
55	0	0	0	0	0	0	0
56	0	0	0	0	0	0	0
57	0	0	0	0	0	0	0
58	0	0	0	0	0	0	0
59	0	0	0	0	0	0	0
60	0	0	0	0	0	0	0
61	0	0	0	0	0	0	0
62	0	0	0	0	0	0	0
63	0	0	0	0	0	0	0
64	7	5	0	0	0	0	12
65	11	0	0	0	0	0	11
66	22	4	0	0	0	0	26
67	36	8	0	0	0	0	44
68	5	2	1	3	5	16	32
69	0	0	0	0	0	7	7
70	0	0	0	0	0	0	0
71	0	0	0	0	0	0	0
72	0	0	0	0	0	0	0
73	0	0	0	0	0	0	0
74	0	0	0	0	0	0	0
75	0	0	0	0	0	0	0
76	0	0	0	0	0	0	0
77	0	0	0	0	0	0	0
78	0	0	0	0	0	0	0
79	0	0	0	0	0	0	0
80	0	0	0	0	0	0	0
81	0	0	0	0	0	0	0
82	0	0	0	0	0	0	0
83	27	4	5	1	1	3	41
84	23	10	8	7	5	15	68
85	19	0	0	0	0	0	19
86	2	0	0	0	0	0	2
87	19	0	0	0	0	0	19

88	0	0	0	0	0	0	0
89	0	0	0	0	0	0	0
90	2	0	0	0	0	0	2
91	1	0	0	0	0	0	1
92	0	0	0	0	0	0	0
93	0	0	0	0	0	0	0
94	0	0	0	0	0	0	0
95	0	0	0	0	0	0	0
96	1	0	0	0	0	0	1
97	0	0	0	0	0	0	0
98	0	0	0	0	0	0	0
99	0	0	0	0	0	0	0
100	0	0	0	0	0	0	0
101	0	0	0	0	0	0	0
102	3	0	0	0	0	0	3
103	0	0	0	0	0	0	0
104	0	0	0	0	0	0	0
105	2	0	0	0	0	0	2
106	0	0	0	0	0	0	0
107	0	0	0	0	0	0	0
108	0	0	0	0	0	0	0
109	0	0	0	0	0	0	0
110	0	0	0	0	0	0	0
111	0	0	0	0	0	0	0
112	0	0	0	0	0	0	0
113	20	13	7	9	3	7	59
114	40	46	0	0	0	0	86
115	0	9	3	4	2	4	22
116	6	2	4	2	4	10	28
117	8	0	0	0	0	0	8
118	3	0	0	0	0	0	3
119	3	0	0	0	0	0	3
120	6	0	0	0	0	0	6
121	0	0	0	0	0	0	0
122	0	0	0	0	0	0	0
123	0	0	0	0	0	0	0
124	0	0	0	0	0	0	0
125	0	0	0	0	0	0	0
126	0	0	0	0	0	0	0
127	0	0	0	0	0	0	0
128	0	0	0	0	0	0	0
129	0	0	0	0	0	0	0
130	0	0	0	0	0	0	0
131	0	0	0	0	0	0	0
132	0	0	0	0	0	0	0
133	0	0	0	0	0	0	0
134	25	6	0	0	0	0	31
135	15	16	9	6	18	148	212
136	53	7	5	7	10	16	98
137	7	5	3	3	5	60	83
138	8	5	10	2	8	26	59
139	6	0	0	0	0	0	6
140	6	0	0	0	0	0	6
141	0	0	0	0	0	0	0
142	0	0	0	0	0	0	0
143	0	0	0	0	0	0	0
144	0	0	0	0	0	0	0
145	0	0	0	0	0	0	0
146	0	0	0	0	0	0	0
147	0	0	0	0	0	0	0
148	0	0	0	0	0	0	0
149	0	0	0	0	0	0	0
150	0	0	0	0	0	0	0

151	0	0	0	0	0	0	0
152	0	0	0	0	0	0	0
153	0	0	0	0	0	0	0
154	0	0	0	0	0	0	0
155	0	0	0	0	0	0	0
156	0	0	0	0	0	0	0
157	0	0	0	0	0	0	0
158	16	24	18	8	0	0	66
159	0	0	0	0	16	9	25
160	0	0	0	0	0	47	47
161	0	0	0	0	0	0	0
162	0	0	0	0	0	36	36
163	1	6	4	5	3	18	37
164	6	7	3	5	9	24	54
165	6	0	0	0	0	0	6
166	0	0	0	0	0	0	0
167	3	0	0	0	0	0	3
168	1	0	0	0	0	0	1
169	4	0	0	0	0	0	4
170	2	0	0	0	0	0	2
171	7	0	0	0	0	0	7
172	0	2	3	1	1	28	35
173	0	0	0	0	0	0	0
174	0	0	0	0	0	0	0
175	0	0	0	0	0	0	0
176	0	0	0	0	0	0	0
177	0	0	0	0	0	0	0
178	0	0	0	0	0	0	0
179	0	0	0	0	0	0	0
180	0	0	0	0	0	0	0
181	0	0	0	0	0	0	0
182	0	0	0	17	48	0	65
183	0	4	0	0	0	0	4
184	0	0	0	0	0	0	0
185	0	0	0	0	0	0	0
186	0	0	0	0	0	0	0
187	0	0	0	0	0	0	0
188	0	0	0	0	0	0	0
189	0	0	0	0	0	0	0
190	0	0	0	0	0	0	0
191	0	0	0	0	0	0	0
192	0	0	0	0	0	0	0
193	0	0	0	0	0	0	0
194	0	0	0	0	0	0	0
195	0	0	0	0	0	0	0
196	0	0	0	0	0	0	0
197	0	0	0	0	0	0	0
198	0	0	0	0	0	0	0
199	0	0	0	0	0	0	0
200	0	0	0	0	0	0	0
201	0	0	0	0	0	0	0
202	0	0	0	0	0	0	0
203	7	0	0	0	0	0	7
204	7	0	0	0	0	0	7
205	0	0	0	0	0	0	0
206	3	0	0	0	0	0	3
207	22	8	10	4	8	18	70
208	30	23	19	17	24	75	188
209	10	8	2	5	4	100	129
210	27	6	0	0	0	0	33
211	2	0	0	0	0	0	2
212	3	0	0	0	0	0	3
213	1	0	0	0	0	0	1

214	5	0	0	0	0	0	5
215	0	0	0	0	0	0	0
216	0	0	0	0	0	0	0
217	0	0	0	0	0	0	0
218	0	0	0	0	0	0	0
219	0	0	0	0	0	0	0
220	0	0	0	0	0	0	0
221	0	0	0	0	0	0	0
222	0	0	0	0	0	0	0
223	0	0	0	0	0	0	0
224	0	0	0	0	0	0	0
225	4	0	0	0	0	0	4
226	0	0	0	0	0	0	0
227	23	2	0	0	0	0	25
228	8	0	0	0	0	0	8
229	0	5	7	8	19	112	151
230	15	8	9	5	17	95	149
231	15	18	6	9	5	23	76
232	0	0	0	0	0	68	68
233	4	28	9	6	14	59	120
234	0	35	0	0	0	0	35
235	0	1	0	0	0	0	1
236	0	0	0	0	0	0	0
237	0	0	0	0	0	0	0
238	0	0	0	0	0	0	0
239	0	0	0	0	0	0	0
240	0	0	0	0	0	0	0
241	0	0	0	0	0	0	0
242	0	0	0	0	0	0	0
243	0	0	0	0	0	0	0
244	0	0	0	0	0	0	0
245	0	0	0	0	0	0	0
246	0	0	0	0	0	0	0
247	0	0	0	0	0	0	0
248	0	0	0	0	0	0	0
249	0	0	0	0	0	0	0
250	0	0	0	0	0	0	0
251	0	0	0	0	0	0	0
252	3	0	0	0	0	0	3
253	9	102	0	0	0	0	111
254	5	12	8	4	16	109	154
255	0	0	0	0	0	0	0
256	0	0	0	0	0	0	0

APPENDIX B

Details of mathematical techniques used during analysis of locomotor activity results.

APPENDIX B

Campbell and Shipp (1974) used a mathematical model with known parameters to illustrate the scope and limitations of the aspects of spectral analysis which are required for the identification of cycles. They followed this with an example of how the technique may be applied in practice. The steps followed in finding the hidden periodicities of the model are summarised below.

1. Removal of any long term trends.
2. Determination of the sample autocorrelation function.
3. Determination of the smoothed spectral density estimate.
4. Interpretation of results.

REMOVAL OF LONG TERM TRENDS

A simplifying assumption of spectral analysis theory is that of stationarity. A stationary time series is one which shows no trends and has an effectively constant mean and variance. In practice, many time series exhibit a marked trend in the mean. In these cases, Campbell and Shipp state that it is possible to remove the non-stationary mean by polynomial regression and substration (Granger, 1964) leaving a series which may be regarded as stationary.

DETERMINATION OF SAMPLE AUTOCORRELATION FUNCTION

Autocorrelation provides a means by which the noise component of a time series can be reduced. At the same time any periodicity

persists and is transformed to a cosine function. As the sample size increases, this effect becomes more pronounced.

The autocovariance function (C_k) for a sample size N and values x_1, x_2, ..., x_n is computed for k lags using the expression,

$$C_k = \frac{1}{N}\left(\sum_{t=1}^{N-K} x_t x_{t+k}\right) \qquad k = 0, 1, 2....., k.$$

DETERMINATION OF THE SMOOTHED SPECTRAL ESTIMATE

The aim of spectral analysis is to obtain an estimate of the theoretical spectrum or periodic component of a time series. This requires the application of both statistical and Fourier analysis, (Campbell and Shipp, 1974).

The Fourier transform of a time series sample might be expected to provide an estimate of its periodic component. The transform is obtained by multiplying and summing through the time series with sine waves of unit amplitude at successive frequencies. When an 'exploring' frequency equals one present in the time series, a peak is produced in the transform. The Fourier transform is a density function and gives the distribution of amplitude with frequency. The Fourier transform however, is an inconsistent estimator and does not produce a better estimate of the theoretical spectrum with increasing sample size (Campbell and Shipp, 1974). For this reason, classical Fourier methods require modification for their application to time series. This is achieved by using the Fourier transform of the sample autocorrelation function. This transform gives an estimate

which converges to the theoretical spectrum, as the size of the time series sample (from which they are calculated) is increased.

The spectral density estimate (R(f)) of a time series is defined by,

$$R(f) = 2(1+2\sum_{K=1}^{N-1} r_k \cos(2\pi fk))$$

Periodicity T = 1/f, thus if data readings are taken at intervals of one hour, the shortest periodicity which can be identified is two hours.

The spectral density estimate formed in this manner, fluctuates about the theoretical spectrum and this instability can be reduced by using a modified or smoothed estimate,

$$\bar{R}(f) = 2(1+2\sum_{K=1}^{L-1} r_k W_k \cos 2\pi fk) \qquad 0 \leq f \leq \tfrac{1}{2}\Delta$$

Where L is the truncation point and W_k is the lag window. Smoothing procedures are discussed by Jenkins and Watts (1968) and Box and Jenkins (1970). The Tukey lag window is commonly quoted in the literature and was used by Campbell and Shipp (1974).

For the Tukey lag window

$$W_k = 0.5(1 + \cos \frac{\pi K}{4})$$

The Fourier transform of the lag window is called the spectral window W(f). For the Tukey window it has a bandwidth,

$$b = \frac{1.33}{L} \qquad \text{(For normalised estimates).}$$

Thus, the smaller the truncation point (L) the wider the bandwidth and the smoother the estimate. This is achieved at the expense of decreased resolution so a compromise must be made between stability and fidelity. Campbell and Shipp (1974) suggest that a sample of 100 or more may be required in order for L to be large enough for high fidelity, and for N/L to be large enough for high stability.

INTERPRETATION OF RESULTS

The bandwidth of the Tukey window is given by,

$$b = \frac{1.33}{L} \times \text{sampling frequency}$$ (for non-normalised estimates).

Peaks falling within this bandwidth of the spectrum cannot be detected, thus if evidence is available which indicates the likelihood of particular periodicities in a time series, the truncation point L should be chosen so that the smoothed spectral density estimate has sufficient fidelity to reveal the expected peaks.

Confidence intervals for a theoretical spectrum can be determined from its smoothed spectral density estimate. The confidence limits about a spectral density of 1.0 are given by,

$$\frac{DF}{X^2_{DF}\ (1-(\frac{\alpha}{2}))} \quad , \quad \frac{DF}{X^2_{DF}\ (\frac{\alpha}{2})}$$

Where the degrees of freedom (DF) for the Tukey lag window = 8/3 N/L and α for 80% confidence intervals, α = 1.0-0.8. If spectral density is plotted on a log scale, the confidence interval line can be

transferred to any point on the spectral density estimate. The theoretical spectrum has then a given probability of lying within each of the confidence intervals.

The theoretical spectrum for a normally distributed random series is a straight horizontal line. Therefore, if a straight horizontal line can be drawn through the confidence intervals of two peaks and the confidence interval of the intervening trough, the peaks cannot be regarded as significant but should be regarded as a consequence of chance fluctuations. In addition, if two peaks are not separated by a width greater than that of the bandwidth, this must also be regarded as a consequence of chance fluctuations.

In the present study, no apparent trends existed in the time series data, and as there was little reason to expect any such trends, the time series were regarded as stationary. No polynomial regression was attempted. Smoothed spectral estimates were obtained for each of the time series by computing the Fourier transform of the sample autocorrelation and using the Tukey lag window. In each case N (Table B-1) was considerably larger than the value of 100 suggested by Campbell and Shipp and in most cases was 256. Campbell and Shipp also suggest that in practice the truncation point L should be less than N/3 in order to avoid instability in the spectral density estimate. In the current study a value of L was always picked in order that $L \leq N/3$.

The values for L and N are shown in Table B.1. In addition, smoothed spectral estimates were not normalised as this was felt to render a more realistic plot. However, as all smoothed spectral estimates

were plotted on a log scale, the bandwidth does not remain constant over the range of the plot. Table B.2 shows the cycles which may be resolved when N = 256 and L = 80, the conditions met in most of the experiments. Only those peaks which may be resolved and which are statistically significant are depicted with confidence intervals.

Table B.1

Experimental parameters for each crab used in investigation into locomotor activity patterns.

Experimental identification	Number of sampling intervals (N)	Truncation point (L)	Sex	Size (mm) carapace width	Collection site
D01	197	60	F	43	I. of Cumbrae
D02	200	65	M	49	I. of Cumbrae
D03	197	60	F	45	I. of Cumbrae
D04	186	60	M	50	I. of Cumbrae
D05	200	65	F	32	I. of Cumbrae
D06	256	80	M	50	I. of Cumbrae
D07	256	80	M	47	I. of Cumbrae
D09	256	80	F	46	I. of Cumbrae
D10	256	80	M	44	I. of Cumbrae
D11	256	80	M	45	I. of Cumbrae
D12	256	80	M	50	I. of Cumbrae
D13	256	80	M	55	Loch Feochan
D14	256	80	F	53	Loch Feochan
All the above experiments were carried out under LD 12:12 conditions.					
T01	256	80	M	40	I. of Cumbrae
T02	256	80	M	40	I. of Cumbrae
T03	256	80	M	45	I. of Cumbrae
T04	240	75	M	48	I. of Cumbrae
T05	122	40	F	45	I. of Cumbrae
T06	256	80	M	44	Loch Feochan
T07	256	80	M	54	Loch Feochan
All 'T0' prefixed experiments were carried out under LD 24:00 conditions.					

Table B.1 continued.

Experimental identification	Number of sampling intervals (N)	Truncation point (L)	Sex	Size (mm) carapace width	Collection site
TD1	256	80	F	44	I. of Cumbrae
TD2	256	80	F	42	I. of Cumbrae
TD3	256	80	M	52	Loch Sween
TD4	256	80	M	52	I. of Cumbrae
TD5	256	80	M	51	I. of Cumbrae
TD6	256	80	M	52	I. of Cumbrae
TD7	256	80	M	33	Loch Sween
TD8	256	80	M	50	Loch Feochan
TD9	256	80	F	42	Loch Feochan
TD10 (T10)	256	80	F	52	Loch Feochan
TD11 (T11)	256	80	M	60	Loch Feochan
TD13 (T13)	256	80	F	49	Loch Sween
TD14 (T14)	256	80	F	50	Loch Sween
TD0	256	80	F	45	I. of Cumbrae

All the above experiments were carried out under LD 00:24 conditions.

Table B.2

Table showing peaks which may be resolved by the bandwidth most commonly encountered in this study where N = 256 and L = 80.

Periodicity (hours)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1	-	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
2		-	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
3			-	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
4				-	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
5					-	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
6						-	-	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
7							-	-	-	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
8								-	-	-	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
9									-	-	-	-	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
10										-	-	-	-	-	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
11											-	-	-	-	-	-	-	Y	Y	Y	Y	Y	Y	Y
12												-	-	-	-	-	-	-	-	Y	Y	Y	Y	Y
13													-	-	-	-	-	-	-	-	-	-	Y	Y
14														-	-	-	-	-	-	-	-	-	-	-
15															-	-	-	-	-	-	-	-	-	-
16																-	-	-	-	-	-	-	-	-

The Y represents periodicities which may be resolved.

APPENDIX C

Computer programs used in analysis of results from locomotor activity experiments.

```
      C  ***  CWGS02.FOR V1.1  -  SUBROUTINE TO RETRIEVE HEADER DATA
      C
0001        SUBROUTINE GETHDR
0002        DIMENSION IBUFF(256)
      C
      C  ***  COMMON BLOCKS COMMUNICATE WITH CALLING PROGRAM
0003        COMMON /EXPT/ NOPTS,NSTGAP,NLEGAP
0004        COMMON /LIGHTS/ ISTTIM(2),INLTST,NLTCNG(10)
0005        COMMON /CRAB/ ISEX,ICARL,ICARW
0006        COMMON /EXIDNT/ IDENT(40)
      C
      C  ***  READ HEADER BLOCK FROM UNIT 1
0007        READ(1'1) (IBUFF(I),I=1,256)
      C
      C  ***  DECODE THE HEADER DATA
0008        NOPTS=IBUFF(1)
0009        NSTGAP=IBUFF(2)
0010        NLEGAP=IBUFF(3)
0011        ISTTIM(1)=IBUFF(65)
0012        ISTTIM(2)=IBUFF(66)
0013        INLTST=IBUFF(67)
0014        DO 20 I=1,10
0015  20    NLTCNG(I)=IBUFF(67+I)
0016        ISEX=IBUFF(129)
0017        ICARL=IBUFF(130)
0018        ICARW=IBUFF(131)
0019        DO 40 I=1,40
0020  40    IDENT(I)=IBUFF(192+I)
      C
      C  ***  RETURN TO CALLING PROGRAM
0021        RETURN
0022        END
```

```
      C  ***  CWGS01.FOR V1.1  -  SUBROUTINE TO INPUT HEADER DATA
      C
0001        SUBROUTINE HEADER
0002        DIMENSION IBUFF(256)
0003        COMMON /EXPT/ NOPTS
      C
      C  ***  GET THE HEADER INFORMATION
0004        WRITE(5,1000)                ! NUMBER OF DATA POINTS
0005        READ(7,2000) IBUFF(1)
0006        NOPTS=IBUFF(1)
0007        WRITE(5,1010)                ! START OF DATA GAP
0008        READ(7,2000) IBUFF(2)
0009        WRITE(5,1020)                ! DATA GAP LENGTH
0010        READ(7,2000) IBUFF(3)
      C
0011        WRITE(5,1080)                ! START TIME OF RUN
0012        READ(7,2020) IBUFF(65),IBUFF(66)
0013        WRITE(5,1030)                ! INITIAL LIGHT STATE
0014        READ(7,2000) IBUFF(67)
0015        DO 20 I=1,10                  ! 10 LIGHT CHANGES
0016        WRITE(5,1040) I
0017  20    READ(7,2000) IBUFF(67+I)
      C
0018        WRITE(5,1050)                ! SEX
0019        READ(7,2000) IBUFF(129)
0020        WRITE(5,1060)                ! CARAPACE LENGTH
0021        READ(7,2010) IBUFF(130)
0022        WRITE(5,1070)                ! CARAPACE WIDTH
0023        READ(7,2010) IBUFF(131)
      C
      C  ***  GET EXPERIMENTAL IDENTIFICATION
0024        WRITE(5,1090)
0025        READ(7,2030) (IBUFF(192+I),I=1,40)
      C
      C  ***  WRITE OUT HEADER BLOCK
0026        WRITE(1'1) IBUFF
      C
      C  ***  RETURN TO CALLING PROGRAM
0027        RETURN
      C
      C  ***  OUTPUT FORMATS
0028  1000  FORMAT('$No of data points?  ')
0029  1010  FORMAT('$Start of data gap?  ')
0030  1020  FORMAT('$Lenght of gap?  ')
0031  1030  FORMAT('$Initial light state?  ')
0032  1040  FORMAT('$Change no (',I2,')?  ')
0033  1050  FORMAT('$Sex?  ')
0034  1060  FORMAT('$Carapace length?  ')
0035  1070  FORMAT('$Carapace width?  ')
0036  1080  FORMAT('$Start time of run?  ')
0037  1090  FORMAT(' Experimental Identification (up to 80 characters)?'/
      C
      C  ***  INPUT FORMATS
0038  2000  FORMAT(I3)
```

```
0039   2010   FORMAT(I2)
0040   2020   FORMAT(2I2)
0041   2030   FORMAT(40A2)
0042          END
```

```
      C  ***  CWGP07.FOR VERSION 1.1  -  3-D PLOT PROGRAM
      C
0001        DIMENSION Z(4320)
      C
      C  ***  FILL ARRAY 'Z' FROM DATA FILE ON DISC
0002        CALL GETDAT(Z)
      C
      C  ***  3-D PLOT THE DATA
0003        CALL PLOTTR
0004        CALL SOLID(Z,240,18,25.0,35.0)
0005        CALL ENDPLT
      C
0006        END
```

```
      C  ***  CWGP06.FOR VERSION 1.1  -  SPECTRUM SMOOTHING PROGRAM
      C
0001        DIMENSION IBUFF(256),FBUFF(256),FAUTOC(256)
0002        DIMENSION A(256),C(256),HRNGE(2),THETA(256)
0003        BYTE FILNAM(16),IDENT,MSSG(32)
0004        DATA FILNAM(15),FILNAM(16)/0,0/
0005        DATA MSSG
           1/10*0,' ','C','H','A','N','N','E','L',' ',0,' ',' ',10*0/
      C
      C  ***  COMMON BLOCKS COMMUNICATE WITH ROUTINE 'GETHDR'
0006        COMMON /EXPT/ NOPTS,NSTGAP,NLEGAP
0007        COMMON /LIGHTS/ ISTTIM(2),INLTST,NLTCNG(10)
0008        COMMON /CRAB/ ISEX,ICARL,ICARW
0009        COMMON /EXIDNT/ IDENT(80)
      C
      C  ***  ANOUNCE THE PROGRAM
0010        WRITE(5,1000)
      C
      C  ***  GET THE FILE AND OPEN IT ON UNIT 1
0011        WRITE(5,1010)
0012        READ(7,2000) (FILNAM(I),I=1,14)
0013        OPEN(UNIT=1,NAME=FILNAM,TYPE='OLD',INITIALSIZE=8,
           1     ACCESS='DIRECT',RECORDSIZE=128)
      C
      C  ***  GET THE HEADER DATA
0014        CALL GETHDR
      C
      C ***  SET UP THE TITLE MESSAGE
0015        DO 10 I=1,10
0016  10    MSSG(I)=IDENT(I)
0017        DO 20 I=1,10
0018  20    MSSG(22+I)=FILNAM(I)
      C
      C  ***  LOOP ROUND FOR EACH CHANNEL
0019        DO 140 NOCHAN=1,7
      C
      C  ***  READ IN DATA
0020        READ(1'NOCHAN+1) (IBUFF(J),J=1,256)
      C
      C ***  WORK OUT THE MEAN OF THE DATA
0021        FTOT=0.0
0022        DO 30 I=1,NOPTS
0023  30    FTOT=FTOT+FLOAT(IBUFF(I))
0024        FMEAN=FTOT/FLOAT(NOPTS)
      C
      C ***  SUBTRACT THE MEAN FROM THE DATA
0025        DO 40 I=1,NOPTS
0026  40    FBUFF(I)=FLOAT(IBUFF(I))-FMEAN
      C
      C  ***  AUTOCORRALATE THE DATA
0027        DO 60 ITAU=1,NOPTS
0028        FAUTOC(ITAU)=0.0
0029        DO 50 J=1,NOPTS-ITAU+1
0030        FPROD=FBUFF(J)*FBUFF(J+ITAU-1)
```

```
0031   50     FAUTOC(ITAU)=FAUTOC(ITAU)+FPROD
0032   60     FAUTOC(ITAU)=FAUTOC(ITAU)/FLOAT(NOPTS)
       C
       C ***  SET UP THE TITLE NUMBER
0033          MSSG(20)=NOCHAN+"60
0034          IF(NOCHAN.EQ.7) MSSG(20)="60
       C
       C ***  PLOT THE AUTOCORROLATION DATA
0036          HRNGE(1)=0.0
0037          HRNGE(2)=FLOAT(NOPTS)
0038          CALL SCOPE
0039          CALL JBAXES
             1(HRNGE,2,12.0,'DELAY',5,
             2FAUTOC,NOPTS,8.0,'ACVF',4)
0040          DO 70 I=1,NOPTS
0041   70     CALL JOIN PT(FLOAT(I),FAUTOC(I))
0042          CALL TITLE(1,2,MSSG,32)
0043          CALL ENDPLT
       C
       C ***  GET LENGTH OF TRUNCATED SERIES
0044   80     WRITE(7,1020)
0045          READ(7,2010) L
0046          IF(L.EQ.0) GO TO 140
0048          NOPLT=-256
0049          IF(L.LT.0) NOPLT=256
0051          L=IABS(L)
       C
       C ***  CALCULATE SMOOTHED SPECTRAL ESTIMATE
0052          DO 90 I=2,L
0053          A(I)=FAUTOC(I)*(1.0+COS(FLOAT(I-1)*3.14159/FLOAT(L)))
0054   90     THETA(I)=2.0*3.14159*FLOAT(I-1)*0.5
0055          DO 100 IFREQ=1,256
0056          C(IFREQ)=FAUTOC(1)
0057          DO 100 I=2,L
0058   100    C(IFREQ)=C(IFREQ)+A(I)*COS(THETA(I)*FLOAT(IFREQ)/256.0)
       C
       C ***  REMOVE ANY ZERO VALUES
0059          DO 110 I=1,256
0060          IF(C(I).GT.0.0) GO TO 110
0062          C(I)=C(I-1)
0063          WRITE(5,1040) I
0064   110    CONTINUE
       C
       C ***  SET UP HORIZONTAL RANGE FOR GRAPH
0065          HRNGE(1)=1.0/128.0
0066          HRNGE(2)=1.0
       C
       C ***  PLOT THE S.S.E. ON THE SCOPE
0067          CALL SCOPE
0068          CALL JBAXES
             1(HRNGE,-2,12.0,'CYCLES/HOUR',11,
             2C(1),NOPLT,8.0,'SMOOTHED SPECTRAL ESTIMATE',26)
0069          DO 120 I=1,256
0070   120    CALL JOIN PT(FLOAT(I)/256.0,C(I))
```

```
0071          CALL TITLE(1,2,MSSG,32)
0072          CALL ENDPLT
      C
      C ***  ASK IF PLOT REQUIRED
0073          WRITE(5,1030)
0074          READ(7,2020) IYN
0075          IF(IYN.NE.2HYE) GO TO 80
      C
      C ***  PLOT THE SMOOTHED SPECTRUM
0077          CALL PLOTTR
0078          CALL JBAXES
             1(HRNGE,-2,20.0,'CYCLES/HOUR',11,
             2C(1),NOPLT,12.0,'SMOOTHED SPECTRAL ESTIMATE',26)
0079          DO 130 I=1,256
0080  130     CALL JOIN PT(FLOAT(I)/256.0,C(I))
0081          CALL TITLE(2,2,MSSG,32)
0082          CALL ENDPLT
0083          GO TO 80
0084  140     CONTINUE
      C
      C  ***  CLOSE THE FILES
0085          CLOSE(UNIT=1)
      C
      C  ***  RETURN TO SYSTEM
0086          CALL EXIT
      C
      C  ***  OUTPUT FORMATS
0087  1000    FORMAT(/' CWGP06 V1.1'/' -----------'/)
0088  1010    FORMAT('$Filename?  ')
0089  1020    FORMAT('$L?  ')
0090  1030    FORMAT('$Plot required?  ')
0091  1040    FORMAT(' Point ',I3,' replaced.')
      C
      C  ***  INPUT FORMATS
0092  2000    FORMAT(14A1)
0093  2010    FORMAT(I4)
0094  2020    FORMAT(A2)
0095          END
```

```
      C  ***  CWGP05.FOR VERSION 1.1  -  FFT PLOT PROGRAM
      C
0001        DIMENSION IBUFF(256),IIMAC(256),FBUFF(256),HRNGE(2)
0002        BYTE FILNAM(16),MSSG(32)
0003        BYTE  IDENT
0004        DATA FILNAM(15),FILNAM(16)/0,0/
0005        DATA MSSG
           1 /10*0,' ','C','H','A','N','N','E','L',' ',0,' ',' ',10*0/
      C
      C  ***  COMMON BLOCKS COMMUNICATE WITH ROUTINE 'GETHDR'
0006        COMMON /EXPT/ NOPTS,NSTGAP,NLEGAP
0007        COMMON /LIGHTS/ ISTTIM(2),INLTST,NLTCNG(10)
0008        COMMON /CRAB/ ISEX,ICARL,ICARW
0009        COMMON /EXIDNT/ IDENT(80)
      C
      C  ***  ANOUNCE THE PROGRAM
0010        WRITE(5,1000)
      C
      C  ***  GET THE FILE AND OPEN IT ON UNIT 1
0011        WRITE(5,1010)
0012        READ(7,2000) (FILNAM(I),I=1,14)
0013        OPEN(UNIT=1,NAME=FILNAM,TYPE='OLD',INITIALSIZE=8,
           1    ACCESS='DIRECT',RECORDSIZE=128)
      C
      C  ***  GET THE HEADER DATA
0014        CALL GETHDR
      C
      C ***  WORK OUT NUMBER OF POINTS TO BE TRANSFORMED
0015        NOTRAN=256
0016        IF(NOPTS.LT.256) NOTRAN=128
      C
      C  ***  SET UP VERTICLE & HORIZONTAL RANGES
0018        DELTF=3600.0/(NOTRAN*1800.0) ! CYCLES/HOUR
0019        HRNGE(1)=DELTF
0020        HRNGE(2)=DELTF*FLOAT(NOTRAN/2)
      C
      C  ***  SET UP THE TITLE MESSAGE
0021        DO 10 I=1,10
0022  10    MSSG(I)=IDENT(I)
0023        DO 20 I=1,10
0024  20    MSSG(22+I)=FILNAM(I)
      C
      C  ***  LOOP ROUND FOR EACH DATA CHANNEL
0025        DO 90 NOPLT=1,7
      C
      C  ***  READ A BLOCK OF DATA
0026        READ(1'NOPLT+1) (IBUFF(I),I=1,256)
      C
      C  ***  WORK OUT THE MEAN OF THE DATA
0027        FTOT=0.0
0028        DO 30 I=1,NOTRAN
0029  30    FTOT=FTOT+FLOAT(IBUFF(I))
0030        FMEAN=FTOT/FLOAT(NOTRAN)
      C
```

```
      C  ***  SUBTRACT THE MEAN FROM THE DATA
0031          DO 40 I=1,NOTRAN
0032  40      IBUFF(I)=IFIX(FLOAT(IBUFF(I))-FMEAN)
      C
      C  ***  SET IMAGINARY FFT DATA TO 0
0033          DO 50 I=1,NOPTS
0034  50      IIMAG(I)=0
      C
      C ***  TRANSFORM THE DATA
0035          CALL FFT(IERROR,NOTRAN,IBUFF,IIMAG,0,ISCALE)
0036          IF(IERROR.NE.0) CALL EXIT
      C
      C ***  SCALE THE DATA AND WORK OUT MODULUS
0038          FSCALE=FLOAT(2**ISCALE)
0039          DO 60 I=1,NOTRAN
0040          FREAL=FLOAT(IBUFF(I))*FSCALE
0041          FIMAG=FLOAT(IIMAG(I))*FSCALE
0042  60      FBUFF(I)=SQRT(FREAL*FREAL+FIMAG*FIMAG)
      C
      C ***  SET UP THE TITLE NUMBER
0043          MSSG(20)=NOPLT+"60
0044          IF(NOPLT.EQ.7) MSSG(20)="60
      C
      C  ***  PLOT THE DATA ON THE SCOPE
0046          CALL SCOPE
0047          CALL JBAXES
             1 (HRNGE,-2,12.0,'CYCLES/HOUR',11,
             2 FBUFF(2),-NOTRAN/2,8.0,'SPECTRAL ESTIMATE',17)
0048          DO 70 I=1,NOTRAN/2
0049  70      CALL JOIN PT(FLOAT(I)*DELTF,FBUFF(I+1))
0050          CALL TITLE(1,2,MSSG,32)
0051          CALL ENDPLT
      C
      C  ***  SEE IF PLOTTER OUTPUT REQUIRED
0052          WRITE(5,1020)
0053          READ(7,2010) IYN
0054          IF(IYN.NE.2HYE) GO TO 90
      C
      C  ***  PLOT THE DATA ON THE PLOTTER
0056          CALL PLOTTR
0057          CALL JBAXES
             1 (HRNGE,-2,20.0,'CYCLES/HOUR',11,
             2 FBUFF(2),-NOTRAN/2,12.0,'SPECTRAL ESTIMATE',17)
0058          DO 80 I=1,NOTRAN/2
0059  80      CALL JOIN PT(FLOAT(I)*DELTF,FBUFF(I+1))
0060          CALL TITLE(2,2,MSSG,32)
0061          CALL ENDPLT
0062  90      CONTINUE
      C
      C  ***  RETURN TO SYSTEM
0063  100     CALL EXIT
      C
      C  ***  OUTPUT FORMATS
0064  1000    FORMAT(/' CWGP06 V1.1'/' -----------'/)
```

```
0065  1010  FORMAT('$Filename?  ')
0066  1020  FORMAT('$Plot required?  ')
      C
      C  ***  INPUT FORMATS
0067  2000  FORMAT(14A1)
0068  2010  FORMAT(A2)
0069        END
```

```
      C  ***  CWGP04.FOR VERSION 1.1  -  CHANNEL 0 DATA PROGRAM
      C
0001        DIMENSION IBUFF(256,6)
0002        BYTE FILNAM(16)
0003        DATA FILNAM(15),FILNAM(16)/0,0/
      C
      C  ***  COMMON BLOCKS COMMUNICATE WITH ROUTINE 'GETHDR'
0004        COMMON /EXPT/ NOPTS,NSTGAP,NLEGAP,NOCHAN
0005        COMMON /EXIDNT/ IDENT(40)
0006        COMMON /LIGHTS/ ISTTIM(2),INLTST,NLTCNG(10)
0007        COMMON /CRAB/ ISEX,ICARL,ICARW
      C
      C  ***  ANOUNCE THE PROGRAM
0008        WRITE(5,1000)
      C
      C  ***  GET THE FILE AND OPEN IT ON UNIT 1
0009        WRITE(5,1010)
0010        READ(7,2000) (FILNAM(I),I=1,14)
0011        OPEN(UNIT=1,NAME=FILNAM,TYPE='OLD',INITIALSIZE=8,
           1     ACCESS='DIRECT',RECORDSIZE=128)
      C
      C  ***  GET THE HEADER DATA
0012        CALL GETHDR
      C
      C  ***  READ IN ALL 6 CHANNELS OF DATA
0013        DO 20 I=1,6
0014  20    READ(1'I+1) (IBUFF(J,I),J=1,256)
      C
      C  ***  SUM THE DATA
0015        DO 30 I=1,NOPTS
0016        DO 30 J=2,6
0017  30    IBUFF(I,1)=IBUFF(I,1)+IBUFF(I,J)
      C
      C  ***  WRITE OUT THE SUMMED DATA
0018        WRITE(1'8) (IBUFF(I,1),I=1,256)
      C
      C ***  CLOSE THE FILES
0019        CLOSE(UNIT=1)
      C
      C  ***  RETURN TO SYSTEM
0020        CALL EXIT
      C
      C  ***  OUTPUT FORMATS
0021  1000  FORMAT(/' CWGP04 V1.1'/' -----------'/)
0022  1010  FORMAT('$Filename?  ')
      C
      C  ***  INPUT FORMATS
0023  2000  FORMAT(14A1)
0024        END
```

```
      C  ***  CWGP03.FOR VERSION 1.1  -  DATA PLOT PROGRAM
      C
0001        DIMENSION IBUFF(256),FBUFF(256),HRNGE(2),VRNGE(2)
0002        BYTE FILNAM(16),MSSG(32)
0003        BYTE  IDENT
0004        DATA FILNAM(15),FILNAM(16)/0,0/
0005        DATA MSSG
           1 /10*0,' ','C','H','A','N','N','E','L',' ',0,' ',' ',10*0/
      C
      C  ***  COMMON BLOCKS COMMUNICATE WITH ROUTINE 'GETHDR'
0006        COMMON /EXPT/ NOPTS,NSTGAP,NLEGAP
0007        COMMON /LIGHTS/ ISTTIM(2),INLTST,NLTCNG(10)
0008        COMMON /CRAB/ ISEX,ICARL,ICARW
0009        COMMON /EXIDNT/ IDENT(80)
      C
      C  ***  ANOUNCE THE PROGRAM
0010        WRITE(5,1000)
      C
      C  ***  GET THE FILE AND OPEN IT ON UNIT 1
0011        WRITE(5,1010)
0012        READ(7,2000) (FILNAM(I),I=1,14)
0013        OPEN(UNIT=1,NAME=FILNAM,TYPE='OLD',INITIALSIZE=8,
           1    ACCESS='DIRECT',RECORDSIZE=128)
      C
      C  ***  CET THE HEADER DATA
0014        CALL GETHDR
      C
      C  ***  SET UP VERTICLE & HORIZONTAL RANGES
0015        HRNGE(1)=0.0
0016        HRNGE(2)=FLOAT(NOPTS)
0017        VRNGE(1)=0.0
0018        VRNGE(2)=150.0
      C
      C  ***  SET UP THE TITLE MESSACE
0019        DO 10 I=1,10
0020  10    MSSG(I)=IDENT(I)
0021        DO 20 I=1,10
0022  20    MSSG(22+I)=FILNAM(I)
      C
      C  ***  LOOP ROUND FOR EACH DATA CHANNEL
0023        DO 60 NOPLT=1,7
      C
      C  ***  READ A BLOCK OF DATA
0024        READ(1'NOPLT+1) (IBUFF(I),I=1,256)
      C
      C  ***  FLOAT THE DATA AND CHECK ITS RANGE
0025        VRNGE(2)=150.0
0026        DO 30 I=1,NOPTS
0027        FBUFF(I)=FLOAT(IBUFF(I))
0028        IF(FBUFF(I).GT.VRNGE(2)) VRNGE(2)=FBUFF(I)
0030  30    CONTINUE
      C
      C ***  SET UP THE TITLE NUMBER
0031        MSSG(20)=NOPLT+"60
```

```
0032          IF(NOPLT.EQ.7) MSSG(20)="60
      C
      C   ***  PLOT THE DATA ON THE SCOPE
0034          CALL SCOPE
0035          CALL JBAXES
             1  (HRNGE,2,12.0,'TIME INTERVAL NUMBER',20,
             2 VRNGE,2,8.0,'NUMBER OF BREAKS',16)
0036          DO 40 I=1,NOPTS
0037    40    CALL JOIN PT(FLOAT(I),FBUFF(I))
0038          CALL TITLE(1,2,MSSG,32)
0039          CALL ENDPLT
      C
      C   ***  SEE IF PLOTTER OUTPUT REQUIRED
0040          WRITE(5,1020)
0041          READ(7,2010) IYN
0042          IF(IYN.NE.2HYE) GO TO 60
      C
      C   ***  PLOT THE DATA ON THE PLOTTER
0044          CALL PLOTTR
0045          CALL JBAXES
             1  (HRNGE,2,20.0,'TIME INTERVAL NUMBER',20,
             2 VRNGE,2,12.0,'NUMBER OF BREAKS',16)
0046          DO 50 I=1,NOPTS
0047    50    CALL JOIN PT(FLOAT(I),FBUFF(I))
0048          CALL TITLE(1,2,MSSG,32)
0049          CALL ENDPLT
0050    60    CONTINUE
      C
      C   ***  RETURN TO SYSTEM
0051    100   CALL EXIT
      C
      C   ***  OUTPUT FORMATS
0052    1000  FORMAT(/' CWGP03 V1.1'/' ----------'/)
0053    1010  FORMAT('$Filename?  ')
0054    1020  FORMAT('$Plot required?  ')
      C
      C   ***  INPUT FORMATS
0055    2000  FORMAT(14A1)
0056    2010  FORMAT(A2)
0057          END
```

```
      C  ***  CWGP02.FOR VERSION 1.1  -  DATA PRINT PROGRAM
      C
0001        DIMENSION IBUFF(256,7)
0002        BYTE FILNAM(16)
0003        DATA FILNAM(15),FILNAM(16)/0,0/
      C
      C  ***  COMMON BLOCKS COMMUNICATE WITH ROUTINE 'GETHDR'
0004        COMMON /EXPT/ NOPTS,NSTGAP,NLEGAP
0005        COMMON /LIGHTS/ ISTTIM(2),INLTST,NLTCNG(10)
0006        COMMON /CRAB/ ISEX,ICARL,ICARW
0007        COMMON /EXIDNT/ IDENT(40)
      C
      C  ***  ANOUNCE THE PROGRAM
0008        WRITE(5,1000)
      C
      C  ***  GET THE FILE AND OPEN IT ON UNIT 1
0009        WRITE(5,1010)
0010        READ(7,2000) (FILNAM(I),I=1,14)
0011        OPEN(UNIT=1,NAME=FILNAM,TYPE='OLD',INITIALSIZE=8,
           1     ACCESS='DIRECT',RECORDSIZE=128)
      C
      C  ***  GET THE HEADER DATA
0012        CALL GETHDR
      C
      C  ***  PRINT THE HEADER DATA
0013        WRITE(6,1020) (FILNAM(I),I=1,14)
0014        WRITE(6,1030) NOPTS
0015        WRITE(6,1040) NSTGAP
0016        WRITE(6,1050) NLEGAP
0017        WRITE(6,1060) ISTTIM(1),ISTTIM(2)
0018        WRITE(6,1070) INLTST
0019        WRITE(6,1080) (NLTCNG(I),I=1,10)
0020        WRITE(6,1090) ISEX
0021        WRITE(6,1100) ICARL
0022        WRITE(6,1110) ICARW
0023        WRITE(6,1120)
0024        WRITE(6,1130) (IDENT(I),I=1,40)
      C
      C  ***  READ IN ALL 6 CHANNELS OF DATA AND INTEGRATED DATA
0025        DO 20 I=1,7
0026  20    READ(1'I+1) (IBUFF(J,I),J=1,256)
      C
      C  ***  PRINT THE DATA ON THE LINE PRINTER
0027        WRITE(6,1140)
0028        DO 40 I=1,NOPTS
0029  40    WRITE(6,1150) I,(IBUFF(I,J),J=1,7)
      C
      C  ***  RETURN TO SYSTEM
0030        CALL EXIT
      C
      C  ***  OUTPUT FORMATS
0031  1000  FORMAT(/' CWGP02 V1.1'/' -----------'/)
0032  1010  FORMAT('$Filename?  ')
0033  1020  FORMAT(' Filename  =  ',14A1///)
```

```
0034   1030  FORMAT(' No. of data points  =  ',I3/)
0035   1040  FORMAT(' Start of data gap   =  ',I3/)
0036   1050  FORMAT(' Length of data gap  =  ',I3///)
0037   1060  FORMAT(' Start time of expt.  =  ',2I2/)
0038   1070  FORMAT(' Initial light state  =  ',I4/)
0039   1080  FORMAT(' Interval numbers of changes in light state:'//
            1       ' ',10(I3,2X)///)
0040   1090  FORMAT(' Sex  =  ',I1/)
0041   1100  FORMAT(' Carapace length  =  ',I2/)
0042   1110  FORMAT(' Carapace width   =  ',I2///)
0043   1120  FORMAT(' Experimental identification:'/)
0044   1130  FORMAT(' ',40A2///)
0045   1140  FORMAT(' Interval No.  ',
            1       'Chan 1  Chan 2  Chan 3  Chan 4  Chan 5  Chan 6'/
            2       ' --------------',
            3       '----------------------------------------------'/)
0046   1150  FORMAT(4X,I3,10X,7(I3,5X))
       C
       C  ***  INPUT FORMATS
0047   2000  FORMAT(14A1)
0048         END
```

```
      C  ***  CWGP01.FOR VERSION 1.1  -  DATA INPUT PROGRAM
      C
0001        DIMENSION IBUFF(256)
0002        BYTE FILNAM(16)
0003        DATA FILNAM(15),FILNAM(16)/0,0/
      C
      C ***  COMMON BLOCK COMMUNICATES WICH ROUTINE 'HEADER'
0004        COMMON /EXPT/ NOPTS
      C
      C  ***  ANNOUNCE THE PROGRAM
0005        WRITE(5,1000)
      C
      C  ***  GET THE FILE AND OPEN IT ON UNIT 1
0006        WRITE(5,1010)
0007        READ(7,2000) (FILNAM(I),I=1,14)
0008        OPEN(UNIT=1,NAME=FILNAM,TYPE='OLD',INITIALSIZE=8,
          1     ACCESS='DIRECT',RECORDSIZE=128)
      C
      C  ***  PROCESS HEADER DATA IF REQUIRED
0009        WRITE(5,1020)
0010        READ(7,2010) IYN
0011        IF(IYN.EQ.2HYE) CALL HEADER
      C
      C  ***  GET THE CHANNEL NUMBER
0013        WRITE(5,1030)
0014        READ(7,2020) NOCHAN
      C
      C  ***  LOOP ROUND TO READ THE DATA POINTS
0015        DO 20 I=1,NOPTS
0016        WRITE(5,1040) I
0017        READ(7,2020) IBUFF(I)
0018        IF(IBUFF(I).GE.0) GO TO 20
0020        NZERO=-IBUFF(I)
0021        DO 10 J=1,NZERO
0022  10    IBUFF(I-1+J)=0
0023        I=I+NZERO-1
0024  20    CONTINUE
0025        IF(NOPTS.EQ.256) GO TO 40
0027        DO 30 I=NOPTS+1,256
0028  30    IBUFF(I)=-1
      C
      C  ***  TYPE OUT THE DATA FOR VERIFICATION
0029  40    WRITE(5,1055)
0030        DO 60 I=1,12
0031        JSTART=(I-1)*20
0032        WRITE(5,1050) JSTART,(IBUFF(J),J=JSTART+1,JSTART+20)
0033        IF(I/5*5.EQ.I) WRITE(5,1055)
0035  60    CONTINUE
0036        WRITE(5,1050) 240,(IBUFF(J),J=241,256),-1,-1,-1,-1
      C
      C  ***  CHECK THAT DATA IS CORRECT
0037        WRITE(5,1060)
0038        READ(7,2010) IYN
0039        IF(IYN.EQ.2HYE) GO TO 80
```

```
      C
      C  ***  CORRECT THE DATA
0041  70     WRITE(5,1070)
0042         READ(7,2020) IBAD
0043         IF(IBAD.EQ.0) GO TO 40
0045         WRITE(5,1080)
0046         READ(7,2020) IBUFF(IBAD)
0047         GO TO 70
      C
      C  ***  WRITE NEW DATA TO FILE AND CLOSE IT
0048  80     WRITE(1'NOCHAN+1) IBUFF
0049         CLOSE(UNIT=1)
      C
      C  ***  EXIT TO THE SYSTEM
0050         CALL EXIT
      C
      C  ***  OUTPUT FORMATS
0051  1000   FORMAT(/' CWGP01 V1.1'/' -----------'/)
0052  1010   FORMAT('$Filename?  ')
0053  1020   FORMAT('$Header?  ')
0054  1030   FORMAT('$Channel?  ')
0055  1040   FORMAT('$Data pt (',I3,')?  ')
0056  1050   FORMAT(1H ,I3,4X,4(5I3,2X))
0057  1055   FORMAT(1H )
0058  1060   FORMAT('$Data correct?  ')
0059  1070   FORMAT('$Bad point?  ')
0060  1080   FORMAT('$Correct value?  ')
      C
      C  ***  INPUT FORMATS
0061  2000   FORMAT(14A1)
0062  2010   FORMAT(A2)
0063  2020   FORMAT(I3)
0064         END
```

APPENDIX D

THE ORGANISATIONAL RELATIONSHIP

BETWEEN PATTERNS IN A FIGHT

APPENDIX D

The orgnaisational relationship between patterns withing a fight.

In this section of the analysis, the standardised interaction length data (rates) described in section 4-3.6, were studied in order to look for groups of behaviour patterns within the original repertoire whose frequencies are correlated and therefore which might share common causal factors. The following categories were studied.

1. Winning crabs
2. Losing crabs
3. Initiating crabs
4. Responding crabs
5. Winning initiators
6. Winning responders
7. Losing initatiors
8. Losing responders
9. Long fights (as defined previously)
10. Intermediate length fights
11. Short fights
12. Winners of long fights
13. Losers of long fights
14. Initiators of long fights
15. Responders in long fights
16. Winners of intermediate fights
17. Losers of intermediate length fights
18. Initiators of intermediate length fights

19. Responders in intermediate length fights
20. Winners of short fights
21. Losers of short fights
22. Initiators of short fights
23. Responders in short fights

Within each category, multiple correlation was carried out between each of the behaviour patterns. Patterns 15 and 16 (Locomotion type and direction of locomotion) were omitted from this analysis as these were not simple parameters. The matrices showing the Spearman Rank Correlation co-efficients for each of the categories are shown at the end of this Appendix. Examination of these matrices shows that a number of behaviour patterns are closely correlated with one another, within a given category, but that there are few consistent trends between different categories. Those trends which do exist are simple and could be predicted by direct observation of the original film. In nearly all cases, Patterns 19 and 20 are correlated with each other. These parameters check whether the swimming legs are in synchronisation with one another. This result suggests that the swimming legs maintain one of two different aspects. Either both swimming legs are held in the same position (synchro nised) or if they are not synchronised they are completely out of synchronisation in both the saggital and the medial plane. Both these possibilities would result in correlation being shown between patterns 19 and 20 and observation of the original film indicates that most of the time the swimming legs are held in the same position. Movement from this position, when it occurred, usually took the form described above, where movement occurred not only in the saggital but the medial plane also, with one leg moving in the opposite direction to the other.

This point is further emphasised when the matrices are studied in more detail. In every category studied, Pattern 14 (swimming leg movement) correlates very strongly with both Pattern 19 and 20, emphasising that when no swimming leg movement occurs, the swimming legs are synchronised and when movement occurs the swimming legs are asynchronised in both the saggital and medial planes. This type of movement is quite characteristic of the movement patterns shown by the crabs, with one swimming leg being moved upwards and forward over the carapace while the other is moved downwards and back from the carapace.

One other set of correlations which occur regularly are those between Pattern 12 (feeding movement) and Pattern 13 (body collapse) and Pattern 12 and Pattern 20 (cheliped synchronisation). The strong correlation between feeding movements and cheliped synchronisation show that the chelipeds are out of synchronisation when these movements occur. Study of the original film also showed that movement of both chelipeds from the substrate to the mouthparts at the same time, very rarely occurred. The correlation between feeding movements and body collapse is a negative relationship in the categories in which it occurs and this probably reflects the fact that feeding movements frequently occur prior to final collapse by a crab and sometimes after a crab raises itself from the substrate at the start of an interaction.

A number of other significant correlations between behaviour patterns can be seen in each of the categories studied. These relationships however do not seem to follow any consistent trend and as such provide little information concerning groups of behaviour patterns with common causal factors.

APPENDIX D

Each of the values in the following correlation matrices is a Spearman Rank Correlation co-efficient (r_s).

As $N > 10$ in each case, the significance of the observed r_s value is determined by computing the t associated with that value, using the formula given below, and then determining the significance of that value by referring to t tables (Seigel, 1956).

$$t = r_s \frac{N-2}{1-r_s^2}$$

Each of the r_s values underlined in the matrices, is significant at $p < 0.05$ (two tailed) ($N = 105$, $r_s = 0.200$, $t = 2.09$, $p < 0.05$)

WINNERS

PATTERN NUMBER	1	2	3	4	5	6	7	8	9	10	11	12	13	14	17	18	19	20
2	0.069																	
3	0.236	-0.006																
4	-0.088	-0.248	0.058															
5	-0.057	0.140	-0.166	-0.033														
6	-0.095	-0.093	0.126	0.149	0.017													
7	0.142	0.070	0.118	-0.155	-0.153	-0.044												
8	-0.088	-0.043	-0.064	-0.018	0.058	0.141	0.202											
9	-0.004	-0.047	-0.038	0.066	-0.182	-0.100	-0.006	-0.064										
10	-0.113	-0.254	-0.127	-0.065	-0.047	0.180	-0.095	-0.012	-0.271									
11	-0.169	-0.166	-0.094	-0.122	-0.166	0.104	0.169	0.101	-0.048	-0.030								
12	-0.071	-0.044	0.052	-0.037	-0.168	-0.174	-0.018	-0.046	0.037	0.021	-0.160							
13	-0.073	-0.124	-0.080	0.026	0.184	0.273	-0.049	0.355	-0.131	-0.119	0.197	-0.125						
14	0.104	0.058	0.060	0.021	-0.032	-0.107	0.063	0.098	-0.002	-0.060	-0.077	0.093	-0.125					
17	-0.114	0.199	0.217	-0.028	0.051	-0.025	0.014	0.047	-0.137	-0.035	0.122	-0.029	-0.101	0.047				
18	-0.052	0.092	-0.126	-0.092	0.138	0.015	0.040	0.106	-0.364	-0.115	-0.031	-0.077	0.193	-0.033	0.046			
19	-0.181	-0.038	0.049	0.099	-0.069	0.076	0.062	0.193	-0.211	0.177	0.049	-0.025	-0.028	0.280	0.179	0.037		
20	0.052	0.064	-0.082	-0.004	-0.089	-0.079	0.026	0.101	-0.016	-0.053	-0.061	-0.100	-0.106	0.735	0.133	0.109	0.382	
21	0.007	-0.007	-0.105	0.090	0.030	-0.147	0.014	-0.131	0.051	-0.144	-0.154	0.207	-0.204	-0.012	0.152	0.079	0.014	0.028

LOSERS

PATTERN NUMBER	1	2	3	4	5	6	7	8	9	10	11	12	13	14	17	18	19	20
2	0.100																	
3	0.045	0.033																
4	0.255	-0.197	-0.096															
5	-0.229	0.063	-0.174	-0.213														
6	-0.007	0.015	0.071	0.013	-0.027													
7	0.038	0.227	0.029	-0.112	-0.104	-0.143												
8	-0.118	-0.129	0.196	-0.085	-0.155	-0.070	0.058											
9	-0.225	-0.044	-0.215	0.043	-0.040	-0.105	0.133	-0.161										
10	-0.170	-0.195	0.006	-0.054	-0.274	0.119	0.016	0.078	-0.112									
11	-0.133	-0.145	-0.049	0.016	-0.174	-0.078	-0.089	0.188	0.092	0.135								
12	-0.021	-0.123	0.053	0.041	-0.109	-0.172	0.160	0.090	0.016	0.191	-0.113							
13	-0.162	-0.205	0.029	-0.025	-0.021	0.033	-0.111	0.001	0.010	-0.189	-0.117	-0.254						
14	0.102	-0.091	0.002	0.056	-0.197	-0.058	0.026	0.012	-0.130	0.149	0.301	-0.114	0.205					
17	-0.020	0.062	-0.096	0.014	-0.038	0.005	-0.043	0.051	0.099	-0.166	-0.096	-0.106	-0.080	-0.002				
18	0.155	0.009	-0.049	0.136	-0.058	-0.078	0.153	0.187	-0.060	-0.131	-0.049	0.081	-0.051	-0.035	0.133			
19	0.042	0.014	-0.014	-0.179	-0.190	0.055	-0.005	0.264	-0.076	0.074	0.029	-0.058	0.297	0.016	-0.040	0.040		
20	0.167	-0.056	0.088	0.062	-0.331	0.086	-0.041	-0.093	-0.208	0.003	0.098	-0.158	0.301	0.591	0.059	-0.017	0.431	
21	0.111	-0.001	-0.060	0.139	-0.037	0.035	-0.054	-0.136	0.082	-0.218	-0.127	0.339	-0.094	-0.151	0.179	-0.051	-0.240	0.019

INITIATORS

PATTERN NUMBER	1	2	3	4	5	6	7	8	9	10	11	12	13	14	17	18	19	20
2	0.012																	
3	0.125	0.046																
4	0.154	-0.272	0.029															
5	-0.185	0.150	-0.204	-0.126														
6	-0.119	-0.061	0.215	0.078	-0.127													
7	0.075	0.204	-0.023	-0.144	-0.087	-0.161												
8	-0.030	-0.109	-0.048	-0.081	-0.046	-0.066	0.254											
9	-0.101	-0.069	-0.077	-0.031	-0.068	-0.058	0.119	0.049										
10	-0.157	-0.242	-0.034	-0.024	-0.372	0.160	-0.004	-0.022	-0.115									
11	-0.175	-0.156	-0.069	-0.022	-0.175	0.024	0.125	-0.041	0.155	0.194								
12	-0.021	-0.050	-0.036	0.028	-0.100	-0.149	0.062	0.047	0.041	0.151	-0.154							
13	-0.130	-0.100	0.054	-0.029	0.072	0.118	-0.101	0.178	-0.069	-0.131	-0.039	-0.189						
14	0.203	-0.023	0.099	0.020	-0.135	-0.165	0.038	0.082	-0.065	0.048	0.137	0.016	0.043					
17	-0.006	0.061	0.125	-0.071	-0.065	0.022	-0.033	0.051	-0.110	-0.111	-0.007	-0.058	-0.163	0.013				
18	0.049	0.055	-0.101	0.052	-0.024	-0.046	0.098	0.120	-0.225	-0.101	-0.086	0.049	0.034	0.014	0.068			
19	-0.147	-0.059	0.279	-0.032	-0.196	0.066	0.049	0.011	-0.270	0.183	0.089	0.111	-0.093	0.247	0.011	0.138		
20	0.220	0.002	0.138	-0.105	-0.240	0.008	0.010	0.064	-0.228	0.001	0.065	-0.111	0.037	0.680	0.086	0.161	0.427	
21	0.126	0.069	-0.058	0.053	-0.009	-0.113	-0.050	-0.120	0.044	-0.215	-0.127	0.297	-0.073	0.013	0.268	-0.043	-0.069	0.074

RESPONDERS

PATTERN NUMBER	2	3	4	5	6	7	8	9	10	11	12	13	14	17	18	19	20
2	0.115																
3	0.118	0.035															
4	-0.044	-0.177	-0.092														
5	-0.112	0.045	-0.153	-0.129													
6	0.027	-0.013	-0.078	0.091	0.123												
7	0.118	0.140	0.019	-0.123	-0.168	-0.006											
8	-0.137	-0.079	0.134	-0.017	-0.065	0.138	0.075										
9	-0.127	-0.013	-0.156	0.124	-0.114	-0.147	-0.008	-0.220									
10	-0.060	-0.188	-0.021	-0.103	-0.007	0.156	-0.057	0.083	-0.294								
11	-0.126	-0.159	0.140	-0.102	-0.169	0.030	-0.006	0.260	-0.104	-0.074							
12	-0.039	-0.130	0.187	-0.003	-0.215	-0.168	0.100	-0.028	-0.003	0.108	-0.124						
13	-0.105	-0.174	-0.142	0.002	0.115	0.060	-0.076	0.032	0.060	-0.272	0.015	-0.292					
14	0.036	0.003	-0.004	0.091	-0.133	0.032	0.037	0.037	-0.074	0.065	0.045	0.014	0.019				
17	-0.141	0.207	-0.008	0.057	0.043	-0.046	0.031	0.055	0.010	-0.020	0.079	-0.052	-0.072	0.058			
18	0.109	0.004	-0.086	-0.087	0.052	0.020	0.063	0.125	-0.296	-0.030	0.021	0.003	-0.096	-0.006	0.115		
19	-0.001	0.002	-0.153	-0.017	-0.094	0.091	-0.008	0.204	-0.213	0.127	0.036	-0.118	0.001	0.358	0.213	0.067	
20	0.011	-0.016	-0.206	0.182	-0.181	0.006	-0.067	-0.021	-0.021	-0.069	-0.035	-0.125	0.176	0.632	0.131	0.049	0.415
21	-0.029	-0.102	-0.162	0.184	0.023	-0.007	0.001	-0.164	0.088	-0.155	-0.148	0.199	-0.104	-0.179	0.010	0.140	-0.161	-0.019

WINNING INITIATORS

PATTERN NUMBER

PATTERN NUMBER

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	17	18	19	20
2	0.128																	
3	0.222	0.009																
4	-0.087	-0.279	0.196															
5	-0.068	0.201	-0.176	-0.049														
6	-0.082	-0.241	0.301	0.176	-0.204													
7	0.106	0.004	-0.127	-0.201	-0.024	-0.174												
8	0.129	-0.085	-0.045	-0.071	0.170	-0.061	0.351											
9	0.124	0.089	0.104	-0.050	-0.126	0.017	0.096	0.201										
10	-0.203	-0.399	-0.143	0.027	-0.241	0.219	-0.177	-0.120	-0.260									
11	-0.182	-0.151	-0.079	-0.126	-0.151	0.124	0.356	-0.038	0.076	0.198								
12	-0.167	-0.005	-0.131	0.032	0.067	-0.143	-0.129	-0.130	-0.017	0.151	-0.230							
13	-0.147	-0.122	-0.064	-0.102	0.136	0.252	-0.088	-0.031	0.046	-0.047	-0.055	-0.016						
14	0.249	0.067	0.112	-0.047	0.099	-0.196	-0.042	0.088	0.070	-0.159	-0.061	-0.006	-0.183					
17	-0.060	-0.169	0.407	-0.107	0.032	-0.028	0.072	-0.076	-0.247	-0.106	0.108	-0.125	-0.109	0.103				
18	-0.187	0.222	-0.116	0.000	0.171	0.037	0.007	-0.056	-0.420	-0.047	-0.100	-0.115	0.234	-0.027	0.058			
19	0.313	-0.030	0.249	0.064	-0.060	0.003	0.101	-0.134	-0.223	0.173	0.174	-0.018	-0.192	0.210	0.100	0.074		
20	0.198	-0.018	0.023	-0.189	-0.029	-0.056	-0.034	0.127	-0.089	-0.083	-0.050	-0.314	0.055	0.758	0.070	0.139	0.275	
21	0.172	0.050	0.039	0.040	0.056	-0.153	-0.065	0.036	-0.040	-0.089	-0.222	0.343	-0.033	0.118	0.249	0.071	-0.030	0.008

d.f. = 45
r_s = 0.28
t = 2.00
p < 0.05

WINNING RESPONDERS

PATTERN NUMBER

PATTERN NUMBER

	2	3	4	5	6	7	8	9	10	11	12	13	14	17	18	19	20
2	-0.004																
3	0.237	-0.014															
4	-0.107	-0.213	-0.102														
5	-0.035	0.088	-0.152	-0.007													
6	-0.120	0.061	-0.083	0.104	0.240												
7	-0.177	0.134	-0.108	-0.116	-0.245	0.078											
8	0.179	-0.039	-0.069	0.014	-0.001	0.265	0.148										
9	-0.105	-0.028	-0.164	0.166	-0.231	-0.200	-0.093	-0.177									
10	0.019	-0.145	-0.110	-0.149	0.085	0.139	-0.062	0.013	-0.267								
11	-0.159	-0.178	0.250	-0.119	-0.178	-0.094	0.026	0.164	-0.128	-0.183							
12	-0.039	-0.102	0.249	-0.075	-0.373	0.188	0.069	-0.050	0.081	-0.081	-0.121						
13	-0.019	-0.133	-0.083	0.102	0.194	-0.320	-0.033	0.440	-0.230	-0.161	0.333	-0.213					
14	0.048	0.024	0.017	0.107	-0.160	0.035	0.133	0.079	-0.034	0.044	-0.089	0.192	-0.111				
17	-0.268	0.247	0.030	0.056	0.036	0.003	-0.021	0.105	-0.070	0.008	0.146	0.009	-0.106	-0.020			
18	0.056	0.002	-0.125	-0.135	0.099	0.014	0.048	0.135	-0.356	-0.141	0.005	-0.082	0.153	-0.055	0.046		
19	-0.077	-0.039	-0.174	0.126	-0.073	0.153	0.037	0.385	-0.194	0.167	-0.052	-0.016	0.089	0.345	0.283	0.029	
20	-0.111	0.107	-0.207	0.175	-0.120	-0.121	0.059	0.104	0.069	-0.018	-0.071	0.097	-0.193	0.676	0.208	0.093	0.482
21	-0.136	-0.075	-0.229	0.149	-0.011	-0.143	0.076	-0.218	0.132	-0.181	-0.100	0.090	-0.318	-0.104	0.061	0.056	0.065	0.072

d.f. = 58
r_s = 0.275
t = 2.00
p < 0.05

LOSING INITIATORS

PATTERN NUMBER

PATTERN NUMBER

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	17	18	19	20
2	-0.064																	
3	0.041	0.067																
4	0.373	-0.264	-0.126															
5	-0.274	0.079	-0.222	-0.173														
6	-0.158	0.093	0.128	-0.027	-0.049													
7	0.043	0.351	0.065	-0.093	-0.138	-0.152												
8	-0.137	-0.128	-0.050	-0.087	-0.154	-0.067	0.185											
9	-0.276	-0.064	-0.226	0.004	-0.053	-0.118	0.139	-0.055										
10	-0.164	-0.120	0.000	-0.071	-0.389	0.091	0.070	0.005	0.018									
11	-0.169	-0.158	-0.061	0.082	-0.190	-0.083	-0.096	-0.043	0.236	0.202								
12	-0.126	-0.061	0.053	0.006	-0.184	-0.196	0.253	0.202	0.055	0.145	-0.071							
13	-0.156	-0.166	0.154	0.003	-0.031	0.130	-0.126	0.226	-0.170	-0.099	-0.032	-0.248						
14	0.153	-0.077	0.104	0.086	-0.295	-0.174	0.103	0.065	-0.184	0.199	0.367	0.061	0.248					
17	-0.067	-0.015	-0.132	-0.033	-0.127	0.078	-0.126	0.146	0.024	-0.158	-0.114	0.014	-0.208	-0.107				
18	0.124	-0.022	-0.080	0.156	-0.099	-0.109	0.198	0.274	-0.057	-0.176	-0.069	0.124	-0.007	-0.043	0.125			
19	0.017	-0.034	0.324	-0.147	-0.253	0.108	-0.019	0.128	-0.317	0.144	0.008	0.199	0.057	0.255	-0.081	0.043		
20	0.255	0.036	0.248	-0.026	-0.348	0.059	0.042	0.037	-0.366	0.057	0.193	0.102	0.174	0.545	0.075	0.049	0.562	
21	0.109	0.054	-0.128	0.067	-0.113	-0.080	-0.012	-0.209	0.117	-0.285	-0.032	0.274	-0.158	-0.038	0.295	-0.076	-0.071	0.179

d.f. = 58
r_s = 0.275
t = 2.00
p < 0.05

LOSING RESPONDERS

PATTERN NUMBER

PATTERN NUMBER

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	18	19	20
2	0.316																
3	-0.088	0.091															
4	0.023	-0.120	-0.080														
5	-0.212	-0.012	-0.154	-0.278													
6	0.258	-0.095	-0.073	0.070	-0.009												
7	0.006	0.157	0.208	-0.145	-0.051	-0.131											
8	-0.088	-0.134	0.500	-0.080	-0.154	-0.073	-0.080										
9	-0.089	0.023	-0.152	0.107	-0.004	-0.004	0.119	-0.260									
10	-0.198	-0.227	0.103	-0.017	-0.125	0.164	-0.080	0.155	-0.265								
11	-0.088	-0.134	-0.044	-0.080	-0.154	-0.073	-0.080	0.4567	-0.087	0.055							
12	-0.235	-0.179	0.133	0.077	-0.026	-0.158	0.141	-0.023	-0.034	0.281	-0.173						
13	-0.076	-0.278	-0.205	-0.024	-0.005	-0.080	-0.076	-0.205	0.186	-0.313	-0.205	-0.302					
14	0.112	-0.040	-0.053	0.044	-0.100	0.099	-0.104	-0.044	-0.099	0.049	0.242	-0.253	0.187				
18	0.018	0.171	-0.073	0.078	0.073	-0.119	0.079	-0.073	0.210	-0.180	-0.073	-0.282	0.156	0.131			
19	0.078	0.056	-0.128	-0.232	-0.115	-0.015	-0.095	-0.128	-0.217	-0.016	0.164	-0.307	0.084	0.362	0.068		
20	0.203	-0.166	-0.205	0.219	-0.253	0.179	-0.235	-0.205	-0.108	-0.082	0.009	-0.421	0.414	0.579	0.073	0.359	
21	0.188	-0.130	-0.077	0.226	0.042	0.142	-0.069	-0.077	0.037	-0.131	-0.225	0.369	-0.025	-0.254	-0.049	-0.444	-0.111

d.f. = 58
r_s = 0.275
t = 2.00
p < 0.05

LONG FIGHTS

PATTERN NUMBER

PATTERN NUMBER

d.f = 58
r_s = 0.26
t = 2.00
p < 0.05

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	17	18	19	20
2	0.109																	
3	0.024	-0.154																
4	0.167	-0.283	-0.092															
5	-0.114	0.187	-0.167	-0.161														
6	-0.164	0.017	-0.062	0.104	0.103													
7	0.093	0.042	-0.110	-0.217	-0.224	-0.094												
8	-0.051	-0.190	0.390	-0.114	-0.126	-0.076	0.204											
9	-0.093	-0.045	-0.243	-0.102	-0.195	-0.096	0.021	-0.118										
10	-0.070	-0.310	0.075	0.026	-0.245	0.113	-0.098	0.033	-0.343									
11	-0.154	-0.154	-0.034	-0.092	-0.167	0.237	0.075	-0.043	0.281	-0.061								
12	-0.082	-0.164	-0.076	-0.042	-0.140	-0.258	0.103	0.043	0.042	0.163	-0.093							
13	0.015	0.081	-0.083	-0.087	0.085	-0.024	-0.002	-0.102	0.199	-0.170	-0.083	-0.058						
14	0.063	-0.034	-0.035	-0.088	-0.033	-0.100	0.054	0.043	0.156	0.132	0.206	0.001	0.023					
17	-0.024	0.187	-0.083	0.032	-0.176	0.028	-0.020	-0.102	-0.134	0.103	-0.083	-0.037	-0.198	0.088				
18	0.090	-0.017	-0.106	0.091	0.043	0.052	0.099	0.060	-0.412	-0.033	-0.106	-0.068	-0.056	0.008	0.200			
19	0.090	-0.104	0.117	0.028	-0.052	0.112	0.097	-0.013	-0.288	0.302	0.091	-0.216	-0.246	0.043	-0.020	0.186		
20	0.094	0.078	-0.000	-0.035	-0.116	-0.158	0.009	0.007	0.194	0.090	0.068	-0.183	-0.048	0.863	0.189	0.026	0.151	
21	-0.125	-0.101	-0.049	-0.025	0.003	0.100	-0.009	0.078	0.076	-0.011	0.235	0.379	-0.284	-0.053	0.168	0.048	0.051	-0.151

INTERMEDIATE LENGTH FIGHTS

PATTERN NUMBER

PATTERN NUMBER

d.f. = 58
r_s = 0.26
t = 2.00
p < 0.05

	2	3	4	5	6	7	8	9	10	11	12	13	14	17	18	19	20
2	-0.081																
3	0.155	0.029															
4	0.139	-0.276	0.100														
5	-0.184	0.101	-0.164	-0.208													
6	0.006	-0.180	0.154	0.153	-0.032												
7	-0.019	0.254	-0.085	-0.089	-0.082	-0.061											
8	-0.154	-0.063	-0.068	-0.039	-0.027	0.104	0.185										
9	-0.141	-0.075	-0.052	0.009	-0.068	-0.042	-0.037	-0.150									
10	-0.077	-0.267	-0.023	-0.047	-0.163	0.412	0.055	0.043	-0.237								
11	-0.124	-0.142	0.195	0.013	-0.146	0.049	-0.075	0.166	-0.021	0.089							
12	-0.004	-0.184	0.009	-0.081	-0.412	-0.107	0.096	0.038	-0.077	0.219	-0.021						
13	-0.128	-0.148	-0.156	0.026	0.212	0.029	-0.058	0.269	-0.058	-0.100	0.063	-0.311					
14	0.191	0.180	-0.046	0.046	-0.108	-0.005	0.046	0.094	-0.314	0.058	0.006	-0.093	0.165				
17	-0.130	0.075	0.225	-0.107	-0.021	-0.060	-0.009	0.176	0.028	-0.165	0.138	0.040	-0.044	0.043			
18	-0.154	0.008	-0.068	-0.153	0.016	-0.125	-0.093	0.282	-0.335	-0.116	0.151	0.096	0.100	0.185	0.135		
19	-0.116	0.086	0.028	-0.065	-0.116	0.028	0.012	0.273	-0.353	0.141	-0.046	0.043	-0.033	0.387	0.086	0.125	
20	0.046	0.114	-0.135	0.020	-0.158	-0.074	-0.003	0.057	-0.246	0.062	0.065	-0.073	0.096	0.774	0.094	0.128	0.458
21	0.105	0.000	-0.143	0.025	-0.130	-0.213	0.121	-0.249	0.101	-0.131	-0.149	0.221	-0.165	-0.091	0.055	-0.008	-0.234	-0.054

SHORT FIGHTS

PATTERN NUMBER	1	2	3	4	5	6	7	8	9	10	11	12	13	14	17	18	19	20
2	0.173																	
3	0.253	0.160																
4	-0.171	-0.156	-0.095															
5	-0.223	-0.035	-0.166	-0.018														
6	-0.019	0.163	0.136	-0.095	-0.068													
7	0.143	0.048	0.064	-0.123	-0.215	-0.103												
8	-0.062	-0.056	-0.034	-0.041	-0.072	-0.034	-0.044											
9	-0.243	-0.204	-0.096	0.215	-0.073	-0.267	0.153	-0.116										
10	-0.229	-0.147	-0.158	-0.190	-0.229	-0.134	0.044	0.166	-0.055									
11	-0.157	-0.143	-0.087	-0.105	-0.184	-0.087	0.205	0.361	-0.019	0.087								
12	-0.115	0.045	0.078	0.166	0.118	-0.207	-0.060	-0.090	0.085	-0.043	-0.229							
13	-0.155	-0.200	0.073	-0.009	0.023	0.236	-0.100	-0.075	-0.001	-0.289	-0.086	-0.241						
14	-0.201	-0.098	0.154	0.173	-0.155	-0.167	0.202	0.041	0.028	-0.026	0.092	0.121	-0.188					
17	0.040	0.165	-0.014	0.072	-0.082	-0.004	0.079	-0.059	-0.056	-0.128	-0.006	-0.118	-0.180	-0.001				
18	0.016	0.043	-0.070	-0.084	-0.147	0.155	0.114	-0.031	-0.060	-0.048	-0.078	-0.081	0.005	0.034	0.015			
19	-0.014	-0.061	0.201	-0.017	-0.232	0.100	0.052	-0.077	-0.116	0.094	0.178	0.012	-0.055	0.368	0.129	0.016		
20	0.286	-0.093	0.139	0.098	-0.308	0.227	0.010	-0.105	-0.139	-0.206	-0.098	-0.153	0.180	0.492	0.079	0.205	0.434	
21	0.077	0.064	-0.025	0.378	0.059	0.069	-0.279	-0.108	0.045	-0.398	-0.275	0.254	0.042	-0.066	0.284	-0.088	-0.088	0.219

d.f. = 66
r_s = 0.24
t = 2.00
$p < 0.05$

WINNERS OF LONG FIGHTS

PATTERN NUMBER	1	2	4	5	6	7	8	9	10	11	12	13	14	17	18	19	20
2	0.279																
4	-0.116	-0.401															
5	0.028	0.260	-0.045														
6	-0.231	-0.007	0.156	0.282													
7	0.137	-0.032	-0.350	-0.481	-0.131												
8	-0.001	-0.196	-0.146	-0.134	-0.119	0.381											
9	0.035	0.037	-0.178	-0.179	-0.215	0.028	0.019										
10	-0.110	-0.120	0.062	-0.155	0.057	-0.198	-0.019	-0.416									
11	-0.163	-0.137	-0.101	-0.181	0.380	0.225	-0.050	0.273	-0.097								
12	-0.146	-0.058	-0.096	-0.382	-0.007	0.157	0.075	-0.044	0.096	-0.200							
13	0.124	-0.002	0.095	0.435	0.091	-0.213	-0.089	0.112	-0.393	-0.062	0.005						
14	-0.033	0.271	-0.189	-0.148	-0.203	0.044	0.160	0.492	-0.152	0.054	-0.096	-0.278					
17	-0.134	0.406	-0.297	0.411	0.024	-0.074	-0.146	-0.247	0.145	-0.101	0.032	-0.181	-0.110				
18	-0.105	0.112	-0.034	0.112	0.023	-0.040	0.114	-0.592	-0.107	-0.137	0.102	-0.065	-0.253	0.162			
19	0.061	-0.058	0.095	-0.119	0.060	0.100	-0.024	-0.277	0.285	-0.172	-0.228	-0.180	-0.321	-0.181	0.091		
20	0.037	0.348	-0.199	-0.089	-0.250	-0.018	0.164	0.364	-0.045	-0.209	-0.173	-0.375	0.917	-0.034	-0.146	-0.140	
21	-0.210	-0.047	-0.173	-0.084	0.021	0.119	0.024	-0.029	0.104	0.271	0.239	-0.135	-0.070	0.200	0.135	0.282	-0.166

d.f. = 28
r_s = 0.31
t = 2.00
$p < 0.05$

INITIATORS OF LONG FIGHTS

PATTERN NUMBER

d.f = 28
r_s = 0.31
t = 2.048
p < 0.05

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	17	18	19	20
2	0.153																	
3	0.170	-0.137																
4	0.285	-0.284	-0.101															
5	-0.345	0.195	-0.163	-0.272														
6	-0.260	0.063	-0.050	0.155	-0.234													
7	0.219	0.219	-0.110	-0.178	-0.128	-0.159												
8	-0.147	-0.137	-0.034	-0.101	0.058	-0.050	0.317											
9	0.037	-0.179	-0.258	-0.253	-0.085	0.102	-0.042	0.183										
10	-0.118	-0.260	0.226	0.248	-0.446	0.140	-0.068	0.075	-0.390									
11	0.181	-0.137	-0.034	-0.101	-0.163	-0.050	-0.110	-0.034	0.291	-0.086								
12	0.070	-0.291	-0.209	0.196	-0.204	-0.088	-0.031	-0.209	0.132	0.259	0.033							
13	0.034	0.001	-0.073	-0.213	0.100	-0.104	-0.043	-0.073	0.127	-0.136	-0.073	0.147						
14	0.249	0.150	0.121	-0.252	0.010	-0.301	0.180	0.253	0.097	-0.048	0.257	-0.122	0.165					
17	0.115	0.258	-0.062	0.114	0.068	-0.0-89	0.251	-0.062	-0.196	-0.040	-0.062	-0.038	-0.130	0.297				
18	-0.001	0.024	-0.101	0.245	-0.031	-0.146	0.197	-0.101	-0.343	-0.018	-0.101	-0.258	0.037	-0.062	0.264			
19	-0.118	0.019	0.320	0.023	-0.153	0.148	0.159	-0.154	-0.344	0.379	0.296	-0.226	-0.325	-0.018	0.068	0.043		
20	0.283	0.177	0.154	-0.231	-0.085	-0.222	0.169	0.273	0.136	-0.081	0.320	-0.314	0.007	0.896	0.303	-0.028	0.151	
21	-0.098	-0.073	-0.238	0.187	0.033	0.388	-0.258	-0.097	0.097	-0.061	0.206	0.284	-0.133	-0.198	0.283	0.029	-0.127	-0.253

RESPONDERS IN LONG FIGHTS

d.f. = 28
r_s = 0.31
t = 2.048
p < 0.05

	2	3	4	5	6	7	8	9	10	11	12	13	14	17	18	19	20
2	0.044																
3	-0.128	-0.172															
4	0.029	-0.258	-0.083														
5	0.171	0.185	-0.172	0.013													
6	-0.069	-0.047	-0.073	0.094	0.395												
7	-0.048	-0.147	-0.110	-0.264	-0.305	-0.043											
8	-0.184	-0.247	0.719	-0.119	-0.247	-0.104	0.119										
9	-0.158	0.099	-0.228	0.053	-0.315	-0.226	0.087	-0.328									
10	-0.144	-0.320	-0.097	-0.147	-0.044	0.015	-0.124	-0.005	-0.309								
11	-0.128	-0.172	-0.034	-0.083	-0.172	0.454	0.262	-0.050	0.272	-0.076							
12	-0.196	-0.076	0.033	-0.235	-0.147	-0.378	0.209	0.185	-0.017	0.083	-0.209						
13	0.022	0.120	-0.092	0.038	0.043	0.002	0.017	-0.132	0.298	-0.265	-0.092	-0.226					
14	-0.194	-0.257	-0.238	0.155	-0.089	0.066	-0.097	-0.139	0.264	0.272	0.162	0.127	-0.109				
17	-0.083	0.170	-0.101	-0.007	0.273	0.070	-0.217	-0.146	-0.068	0.215	-0.101	-0.088	-0.271	-0.117			
18	0.195	-0.055	-0.110	-0.052	0.143	0.163	-0.003	0.158	-0.484	-0.042	-0.110	0.105	-0.156	0.097	0.163		
19	0.281	-0.223	-0.110	-0.002	0.119	0.133	0.001	0.119	-0.176	0.246	-0.110	-0.229	-0.156	0.100	-0.021	0.342	
20	-0.104	-0.003	-0.190	0.231	-0.115	-0.115	-0.205	-0.102	0.280	0.209	-0.190	-0.055	-0.119	0.811	0.063	0.104	0.161
21	-0.076	-0.155	0.118	-0.271	-0.034	-0.122	0.237	0.155	0.103	-0.033	0.269	0.458	-0.431	0.042	-0.019	-0.001	0.242	-0.149

LOSERS OF LONG FIGHTS

PATTERN NUMBER

PATTERN NUMBER

d.f. = 28
r_s = 0.31
t = 2.048
p< 0.05

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	17	18	19	20
2	0.062																	
3	0.070	-0.247																
4	0.458	-0.144	-0.119															
5	-0.240	0.157	-0.222	-0.274														
6	-0.145	0.172	-0.050	-0.083	-0.154													
7	0.028	0.134	-0.146	-0.049	0.052	-0.101												
8	-0.145	-0.172	0.670	-0.083	-0.154	-0.034	-0.101											
9	-0.214	-0.178	-0.387	-0.005	-0.203	0.204	0.045	-0.269										
10	-0.128	-0.419	0.225	-0.093	-0.415	-0.022	-0.170	0.033	-0.172									
11	-0.145	-0.172	-0.050	-0.083	-0.154	-0.034	-0.101	-0.034	0.290	-0.022								
12	-0.012	-0.330	-0.109	-0.008	0.022	-0.219	0.076	0.077	0.111	0.326	0.055							
13	-0.038	0.093	-0.146	-0.243	-0.192	-0.101	0.202	-0.101	0.230	0.092	-0.101	-0.099						
14	0.091	-0.196	0.059	-0.055	0.010	-0.172	-0.020	-0.172	-0.035	0.294	0.332	0.218	0.358					
17	0.056	0.033	-0.089	0.524	-0.078	-0.062	0.012	-0.062	0.054	-0.063	-0.062	-0.055	-0.181	0.227				
18	0.296	-0.062	-0.104	0.312	-0.065	-0.073	0.228	-0.073	-0.113	-0.172	-0.073	-0.155	0.039	0.120	0.182			
19	0.079	0.039	0.267	-0.049	0.024	-0.092	0.030	-0.092	-0.146	0.050	0.414	-0.183	-0.271	0.279	0.066	0.001		
20	0.094	-0.061	0.099	0.161	-0.214	-0.137	-0.036	-0.137	0.185	0.101	0.360	-0.158	0.378	0.763	0.421	0.028	0.355	
21	-0.037	-0.174	-0.095	0.180	0.057	0.291	-0.170	0.140	0.160	-0.065	0.162	0.533	-0.439	-0.052	0.129	-0.026	-0.207	0.219

WINNERS OF INTERMEDIATE LENGTH FIGHTS

PATTERN NUMBER

d.f. = 41
r_s = 0.30
t = 2.00
p < 0.05

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	17	18	19	20
2	-0.126																	
3	0.236	0.004																
4	-0.042	-0.252	0.173															
5	-0.239	0.278	-0.159	-0.074														
6	-0.026	-0.250	0.199	0.204	-0.074													
7	-0.009	0.128	0.131	-0.008	0.009	0.009												
8	-0.174	-0.030	-0.116	0.025	0.241	0.219	0.127											
9	0.015	-0.198	-0.081	0.067	-0.189	-0.096	-0.103	-0.186										
10	0.051	-0.274	-0.043	-0.108	-0.106	0.435	0.027	0.084	-0.328									
11	-0.149	-0.194	-0.212	-0.130	-0.120	0.108	-0.009	0.248	-0.136	0.040								
12	0.158	-0.197	0.040	-0.216	-0.444	-0.185	0.081	-0.107	0.129	0.111	-0.051							
13	-0.174	-0.227	-0.116	0.025	0.307	0.229	0.139	0.697	-0.274	0.090	0.219	-0.113						
14	0.054	0.125	-0.090	0.013	0.134	-0.018	0.074	0.146	-0.387	0.027	-0.089	-0.074	0.115					
17	-0.054	0.124	0.289	-0.049	-0.052	-0.032	0.121	0.164	-0.176	-0.067	0.254	-0.034	-0.020	0.195				
18	-0.197	0.021	-0.131	-0.172	0.277	-0.172	-0.131	0.126	-0.430	-0.096	0.158	0.005	0.383	0.207	0.034			
19	-0.264	0.063	0.012	0.154	0.063	0.161	0.080	0.360	-0.256	0.163	-0.025	-0.092	0.147	0.448	0.212	0.064		
20	-0.054	0.142	-0.192	0.003	-0.016	-0.125	-0.025	0.139	-0.230	-0.107	0.000	-0.135	-0.072	0.786	0.308	0.150	0.551	
21	0.207	-0.007	-0.189	-0.010	-0.248	-0.285	0.055	-0.259	0.065	-0.234	-0.221	0.241	-0.259	0.001	-0.124	0.087	-0.233	0.002

LOSERS OF INTERMEDIATE LENGTH FIGHTS

d.f. = 41
r_s = 0.30
t = 2.00
p < 0.05

	1	2	4	5	6	7	8	9	10	11	12	13	14	17	18	19	20
2	-0.031																
3	0.303	-0.295															
4	-0.199	0.012	-0.330														
5	0.028	-0.107	0.107	0.030													
6	-0.019	0.379	-0.163	-0.143	-0.140												
7	-0.128	-0.128	-0.113	-0.193	-0.097	0.274											
8	-0.307	0.085	-0.050	0.007	0.022	0.028	-0.094										
9	-0.205	-0.262	0.006	-0.208	-0.386	0.095	0.003	-0.155									
10	-0.089	-0.089	0.245	-0.135	-0.068	-0.049	-0.034	0.176	0.199								
11	-0.138	-0.238	0.075	-0.270	-0.068	0.144	0.232	-0.374	0.341	-0.110							
12	-0.143	-0.098	-0.002	-0.028	-0.044	-0.159	0.157	0.098	-0.194	0.060	-0.306						
13	0.339	0.248	0.073	-0.279	-0.018	0.025	0.013	-0.230	0.084	0.200	-0.168	0.273					
14	-0.203	0.015	-0.158	0.067	-0.098	-0.163	0.182	0.284	-0.277	-0.079	0.046	-0.028	-0.151				
17	-0.089	-0.089	-0.079	-0.135	-0.068	-0.048	0.715	-0.195	-0.167	-0.024	0.219	0.087	0.125	0.323			
18	0.041	0.128	-0.289	-0.262	-0.156	-0.070	0.120	-0.474	0.103	-0.130	0.211	-0.097	0.301	-0.073	0.287		
19	0.163	0.116	0.044	-0.317	-0.044	0.060	-0.039	-0.273	0.236	0.212	0.006	0.207	0.773	-0.178	0.086	0.354	
20	0.012	0.020	0.035	-0.065	-0.115	0.174	-0.223	0.122	-0.019	-0.026	0.245	-0.203	-0.188	0.235	-0.156	-0.222	-0.115

INITIATORS OF INTERMEDIATE LENGTH FIGHTS

PATTERN NUMBER

d.f. = 41
r_s = 0.30
t = 2.00
$p < 0.05$

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	17	18	19	20
2	−0.147																	
3	0.122	0.037																
4	0.161	−0.353	0.205															
5	−0.091	0.255	−0.176	−0.242														
6	−0.044	−0.188	0.327	0.069	−0.128													
7	−0.076	0.364	−0.088	−0.185	−0.032	−0.163												
8	−0.150	−0.135	−0.060	−0.128	−0.142	−0.113	0.274											
9	−0.293	0.106	0.043	−0.103	−0.043	−0.032	0.053	−0.077										
10	−0.146	−0.281	−0.076	−0.093	−0.322	0.413	0.088	−0.001	−0.085									
11	−0.150	−0.135	−0.060	0.082	−0.142	0.163	−0.071	−0.049	0.278	0.241								
12	0.055	−0.082	0.000	−0.104	−0.360	−0.097	0.111	0.207	−0.075	0.163	−0.164							
13	−0.188	−0.156	−0.167	−0.081	0.138	−0.030	−0.029	0.331	0.021	−0.001	0.057	−0.292						
14	0.307	0.025	0.034	0.148	−0.289	−0.028	0.011	−0.005	−0.538	0.156	−0.016	−0.015	0.032					
17	−0.086	−0.028	0.334	−0.082	−0.106	0.006	−0.174	0.156	0.038	−0.221	−0.120	0.069	−0.138	−0.095				
18	−0.185	0.199	−0.075	−0.158	0.018	−0.140	−0.088	0.362	−0.356	−0.199	−0.060	0.196	0.006	0.332	0.241			
19	−0.151	−0.006	0.198	−0.001	−0.198	0.042	−0.079	0.096	−0.393	0.202	−0.179	0.099	−0.123	0.322	−0.013	0.257		
20	0.069	0.096	−0.064	0.047	−0.272	−0.006	0.060	−0.020	−0.533	0.232	0.071	−0.097	−0.045	0.846	0.007	0.352	0.430	
21	0.107	0.151	−0.086	−0.095	−0.157	−0.281	0.154	−0.208	−0.041	−0.159	−0.107	0.323	−0.038	0.051	0.177	−0.004	−0.243	0.055

RESPONDERS IN INTERMEDIATE LENGTH FIGHTS

d.f. = 41
r_s = 0.30
t = 2.00
$p < 0.05$

	2	3	4	5	6	7	8	9	10	11	12	13	14	17	18	19	20
2	0.013																
3	0.179	0.014															
4	0.004	−0.171	−0.089														
5	−0.297	−0.044	−0.150	−0.153													
6	0.020	−0.163	−0.089	0.242	0.090												
7	0.053	0.156	−0.080	0.039	−0.133	0.077											
8	−0.140	−0.019	−0.071	0.071	0.051	0.331	0.127										
9	0.028	−0.219	−0.157	0.143	−0.009	−0.069	−0.131	−0.212									
10	0.017	−0.252	0.039	−0.001	−0.014	0.411	0.033	0.072	−0.396								
11	−0.097	−0.150	0.475	−0.089	−0.150	−0.089	−0.080	0.326	−0.255	−0.050							
12	0.034	−0.295	0.218	0.019	−0.481	−0.095	0.104	−0.094	−0.101	0.260	0.058						
13	−0.046	−0.127	−0.142	0.151	0.266	0.128	−0.086	0.231	−0.029	−0.214	0.055	−0.332					
14	0.115	0.308	−0.103	−0.071	0.037	0.052	0.070	0.159	−0.144	−0.033	0.032	−0.137	0.258				
17	−0.167	−0.190	0.118	−0.134	0.064	−0.143	0.150	0.193	−0.002	−0.118	0.399	−0.006	0.053	0.187			
18	−0.120	0.185	−0.060	−0.110	0.009	−0.110	−0.099	0.232	−0.315	−0.030	0.343	0.049	0.182	0.067	0.050		
19	−0.101	0.197	−0.186	−0.146	−0.036	0.033	0.120	0.430	−0.336	0.079	0.077	0.005	0.062	0.451	0.197	−0.018	
20	0.048	0.130	−0.201	−0.014	−0.045	−0.124	−0.065	0.105	−0.035	−0.098	0.075	−0.105	0.239	0.717	0.182	−0.027	0.470
21	0.081	−0.158	−0.193	0.188	−0.099	−0.141	0.059	−0.280	0.187	−0.095	−0.193	0.154	−0.290	−0.188	−0.077	0.003	−0.234	−0.148

WINNERS OF SHORT FIGHTS

PATTERN NUMBER

d.f. = 32
r_s = 0.31
t = 2.021
$p < 0.05$

	1	2	3	4	5	6	7	9	10	11	12	13	14	17	18	19	20
2	0.164																
3	0.454	-0.103															
4	-0.200	-0.151	-0.091														
5	-0.138	-0.056	-0.137	-0.024													
6	-0.095	-0.072	-0.044	-0.063	-0.095												
7	0.209	0.082	-0.091	-0.133	-0.200	-0.063											
9	-0.184	-0.093	-0.021	0.299	-0.235	-0.154	-0.011										
10	-0.291	-0.325	-0.249	-0.171	-0.071	0.071	-0.022	-0.001									
11	-0.170	-0.129	-0.078	-0.113	-0.170	-0.054	0.472	-0.074	-0.036								
12	-0.195	0.199	0.048	0.273	0.247	-0.154	-0.146	0.059	-0.151	-0.275							
13	-0.137	-0.103	-0.062	-0.091	-0.137	0.781	-0.091	-0.221	-0.121	0.374	-0.221						
14	0.241	-0.124	0.365	0.176	-0.058	-0.200	0.162	0.159	-0.321	-0.070	0.262	-0.287					
17	-0.172	0.144	0.120	0.226	-0.001	-0.095	0.049	0.031	-0.194	0.104	-0.055	-0.137	-0.023				
18	-0.024	0.120	-0.091	-0.133	-0.200	0.428	0.165	-0.032	-0.199	-0.113	-0.218	0.272	0.048	-0.016			
19	-0.135	-0.170	0.131	0.058	-0.161	-0.132	0.102	-0.069	0.072	0.211	0.019	-0.189	0.416	0.239	-0.025		
20	0.182	-0.195	0.105	0.119	-0.183	0.225	0.085	0.021	-0.170	-0.064	-0.076	0.064	0.635	0.026	0.315	0.437	
21	-0.208	0.073	0.036	0.415	0.197	-0.139	-0.291	0.209	-0.283	-0.249	0.248	-0.200	0.050	0.452	-0.071	0.107	0.108

LOSERS OF SHORT FIGHTS

d.f. = 32
r_s = 0.31
t = 2.021
$p < 0.05$

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	17	19	20
2	0.231																
3	0.089	0.321															
4	-0.143	-0.157	-0.097														
5	-0.291	-0.029	-0.197	-0.007													
6	0.070	0.254	0.196	-0.113	-0.091												
7	0.055	0.020	0.198	-0.113	-0.231	-0.133											
8	-0.080	-0.088	-0.054	-0.054	-0.110	-0.063	-0.063										
9	-0.260	-0.312	-0.166	0.186	0.034	-0.369	0.299	-0.176									
10	-0.190	0.019	-0.087	-0.261	-0.361	-0.170	0.136	0.273	-0.049								
11	-0.143	-0.157	-0.097	-0.097	-0.197	-0.113	-0.113	0.523	0.019	0.207							
12	0.010	-0.018	0.218	0.025	-0.035	-0.215	0.095	-0.103	0.272	-0.065	-0.184						
13	-0.117	-0.346	0.092	0.087	-0.036	0.041	-0.082	-0.161	0.045	-0.274	-0.288	-0.127					
14	0.1040;0·081		-0.023	0.178	-0.238	-0.162	0.241	0.063	-0.059	0.091	0.284	-0.063	-0.179				
17	0.270	0.197	-0.129	-0.129	-0.146	0.069	0.121	-0.072	-0.117	-0.138	-0.129	-0.244	-0.151	0.033			
19	0.128	0.068	0.339	-0.157	-0.320	0.295	0.005	-0.088	-0.101	-0.037	0.134	-0.165	0.226	0.328	-0.037		
20	0.408	-0.009	0.145	0.118	-0.420	0.225	-0.065	-0.154	-0.258	-0.271	-0.126	-0.210	0.264	0.365	0.154	0.499	
21	0.392	0.049	-0.091	0.385	-0.090	0.135	-0.277	-0.169	-0.073	-0.465	-0.301	0.392	0.034	-0.151	0.158	-0.255	0.311

INITIATORS OF SHORT FIGHTS

PATTERN NUMBER

d.f. = 32
r_s = 0.31
t = 2.021
p< 0.05

	1	2	3	4	5	6	7	9	10	11	12	13	14	17	18	19	20
2	0.083																
3	0.258	0.037															
4	-0.137	-0.137	-0.078														
5	-0.233	0.021	-0.210	0.282													
6	-0.170	0.122	0.267	-0.078	-0.033												
7	-0.023	-0.200	-0.113	-0.091	-0.246	-0.113											
9	-0.094	-0.335	-0.099	0.229	-0.045	-0.262	0.298										
10	-0.371	-0.244	-0.278	-0.097	-0.464	-0.209	0.147	0.149									
11	-0.170	-0.170	-0.097	-0.078	-0.210	-0.097	0.509	0.103	0.231								
12	-0.185	0.067	-0.054	0.178	0.197	-0.210	-0.124	0.013	0.032	-0.210							
13	-0.109	-0.099	0.391	0.155	-0.005	0.438	-0.168	-0.314	-0.214	-0.143	-0.195						
14	0.225	-0.165	0.132	0.200	-0.107	-0.329	0.165	0.242	-0.000	0.177	0.113	-0.143					
17	0.146	0.147	-0.007	-0.148	-0.092	0.026	0.025	-0.117	-0.156	0.066	-0.138	-0.272	-0.033				
18	-0.095	-0.095	-0.054	-0.043	-0.117	0.577	-0.063	-0.147	0.072	-0.054	-0.117	0.441	-0.184	-0.103			
19	-0.086	-0.140	0.499	-0.169	-0.198	0.018	0.189	-0.131	0.047	0.272	0.252	0.002	0.310	-0.014	-0.117		
20	0.491	-0.096	0.439	-0.210	-0.336	0.140	0.015	-0.160	-0.191	-0.093	-0.076	0.111	0.489	0.117	0.205	0.415	
21	0.307	0.125	0.154	0.224	0.081	-0.076	-0.029	0.073	0.495	-0.262	0.291	-0.099	0.088	0.368	-0.147	0.056	0.275

RESPONDERS IN SHORT FIGHTS

d.f. = 32
r_s = 0.31
t = 2.021
p< 0.05

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	17	18	19	20
2	0.261																	
3	0.248	0.342																
4	-0.190	-0.151	-0.103															
5	-0.232	-0.184	-0.126	-0.209														
6	0.155	0.251	-0.062	-0.103	-0.126													
7	0.342	0.429	0.272	-0.151	-0.184	-0.091												
8	-0.080	-0.063	-0.043	-0.072	-0.088	-0.043	-0.063											
9	-0.383	0.032	-0.074	0.182	-0.070	-0.264	0.006	-0.184										
10	-0.090	-0.057	-0.020	-0.235	-0.007	-0.059	-0.076	0.278	-0.220									
11	-0.143	-0.113	-0.078	-0.128	-0.157	-0.078	-0.113	0.523	-0.115	-0.060								
12	0.020	0.020	0.260	0.150	0.016	-0.200	0.011	-0.139	0.113	-0.117	-0.249							
13	-0.169	-0.276	-0.189	-0.143	0.090	0.081	-0.039	-0.132	0.159	-0.322	-0.050	-0.321						
14	0.203	0.027	0.189	0.150	-0.233	0.041	0.251	0.054	-0.209	-0.028	0.006	0.122	-0.287					
17	-0.168	0.132	-0.091	0.375	-0.184	-0.091	0.165	-0.063	0.069	-0.169	-0.113	-0.115	-0.010	0.040				
18	0.104	0.236	-0.078	-0.128	-0.157	-0.078	0.215	-0.054	-0.061	-0.086	-0.097	-0.089	-0.235	0.170	0.196			
19	0.061	-0.003	-0.148	0.105	-0.298	0.163	-0.064	-0.103	-0.090	0.132	0.082	-0.246	-0.062	0.426	0.324	0.102		
20	0.046	-0.143	-0.221	0.305	-0.278	0.339	0.001	-0.154	-0.13	-0.221	-0.097	-0.231	0.249	0.492	0.003	0.221	0.453	
21	-0.183	-0.048	-0.232	0.499	0.033	0.216	-0.338	-0.161	0.011	-0.300	-0.288	0.222	0.115	-0.233	0.208	-0.061	-0.220	0.165

BEHAVIOUR PATTERN SUMMARY SHEET

Pattern No.	Description
1	Body fully tilted and fully raised. Chelipeds extended, level with carapace, chelae open. Swimming legs raised, extended, paddle angle straight.
2.	As for Pattern 1, except paddle angle bent, not straight.
3	Body fully tilted and fully raised. Chelipeds extended, level with carapace, chelae open. Swimming legs extended, paddle angle straight, not raised.
4	Body slightly tilted, partially raised. Chelipeds extended, level with carapace, chelae open. Swimming legs raised, extended, paddle angle straight.
5	As for Pattern 4, except paddle angle bent.
6	Body slightly tilted, partially raised. Chelipeds extended, level with carapace, chelae open. Swimming legs not raised, not extended, paddle bent.
7	Body fully tilted, fully raised. Chelipeds down, chelae open. Swimming legs raised, extended, paddle straight.
8	As for Pattern 7, except swimming legs not extended, not raised and paddle bent.
9	As for Pattern 7, except body slightly tilted and partially raised.
10	Body slightly tilted, partially raised. Chelipeds down, chelae open. Swimming legs not extended, not raised, paddle bent.
11	Body slightly tilted, partially raised. Chelipeds folded. Swimming legs not raised, not extended, paddle bent.
12	Feeding movements.
13	Collapsed on substrate.
14	Swimming leg movement.
15	Locomotion type.
16	Direction of locomotion relative to opponent.
17	Strike opponent.
18	Grasp opponent.
19	Asynchrony of swimming legs in medial plane.
20	Asynchrony of swimming legs in saggital plane.
21	Asynchrony of chelipeds.